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Autecological Characteristics of Selected Species that Compete with Conifers in British Columbia: A Literature Review

by

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1 INTRODUCTION

The term **autecology** combines the prefix **auto** (meaning "self") with **ecology** and refers literally to the ecology of an individual organism. Plant autecology is the study of those aspects of the ecology of a plant species or population that involve interactions between the plant and its environment (Daubenmire 1974). It is distinct from **synecology,** the other main branch of plant ecology, which describes plant communities and the interactions among plant species.

Most foresters are already familiar with the subject of autecology as it relates to tree species, but they usually use the term **silvics**. The two terms are synonymous except that autecology does not limit itself to tree species.

The need for more information about the autecology of major species of competing vegetation in British Columbia was identified by Conard (1984) in a problem analysis of vegetation management research needs in this province.

Competing vegetation has a major impact on the establishment and growth of crop trees in British Columbia. The problem has existed for some time, but most silviculturists, particularly in the interior and northern areas of the province, are just now beginning to look seriously for techniques of managing competing vegetation to successfully regenerate logged areas and rehabilitate backlog sites. Lack of basic information about the ecology of the plant species that compete with crop trees, and about how these species react to silvicultural treatments, significantly impairs the silviculturist's ability to select and apply appropriate treatments.

The ecosystem classification system used by the B.C. Ministry of Forests provides a framework for describing the vegetation complexes that develop following forest harvesting and the various environments in which they grow. The process of characterizing seral plant communities has begun, but it will be some time before forest ecologists and silviculturists will be able make informed predictions about the development of vegetation on different ecosystems following harvesting.

In the meantime, it is equally important to identify and understand the individual species that make up the vegetation complexes that compete with crop trees. Foresters have tended to consider all shrub and herbaceous vegetation as just "brush". This publication aims to make foresters more aware of some of the differences that exist among these various species of brush.

Thirty-one species are included in this publication. They include hardwood trees, shrubs, and some herbaceous plants. Some of the species are widely distributed and compete with coniferous tree growth throughout British Columbia, while others create only localized silvicultural problems. The list, compiled with assistance from Regional silviculturists and ecologists, includes major competing species from all Forest Regions, but emphasizes species that are a concern in the northern and interior areas of the province.

The autecological information presented here focuses specifically on the management of these species as silvicultural "weeds" that interfere with the growth of coniferous tree species. Deciduous trees, shrubs, and herbaceous plants play a very important role in the function of natural ecosystems. They can also be directly beneficial to man: as forage and cover for wildlife and livestock; as anchor species for reclamation of disturbed sites, erosion control, and streambank stabilization; as ornamentals and nurse crops; and as crops in their own right. These many values of vegetation are not considered in this publication, except when it appears that they may be of benefit to the growth of crop trees.

No original research was carried out for this publication. It is a literature review, containing information gathered in an extensive search of ecological, silvicultural, and botanical literature pertaining to the selected species. Most of the literature originates in Canada or the western United States. Some English-language literature from western Europe and further abroad is included for certain circumpolar species.

For many of the species, there is little published information relevant to British Columbia. Personal communications and unpublished reports have therefore been used throughout this report to supplement the literature. Interviews were conducted with forest ecologists, silviculturists, botanists, and researchers in vegetation management throughout British Columbia and in the northwestern U.S., and much of the information they gave was incorporated into the report. The result is a more complete picture of what is known about the autecology of these plant species in the British Columbia environment.

2 EXPLANATORY NOTES

This section of the report outlines the format used to present information about each of the plant species and provides some explanatory notes for each of the topics under discussion. It is not intended to serve as a detailed review of basic principles of autecology.

The format used to present information about individual species is a modified version of the format developed for the "Biological Flora of the British Isles" series in the Journal of Ecology (see, for example, Myerscough 1980) and subsequently adopted by the Canadian Field-Naturalist for its series "The Biological Flora of Canada" (Hall *et al.* 1979). Certain topics beyond the scope of this literature review were eliminated, and others were adapted to suit the silvicultural slant of this publication.

2.1 Description

This introductory paragraph gives a brief botanical description of the plant including its growth form or habit, and stem, leaf, flower, and fruit characteristics. The description and accompanying figure are not sufficiently detailed to enable the reader to positively identify the plant species. Readers experiencing difficulties in identifying a particular species of competing vegetation should refer to one of the plant identification handbooks produced by the B.C. Ministry of Forests, or to the reference flora cited at the end of the description.

2.1.1 Variation

A plant species is typically composed of a mosaic of populations, each of which differs in genetically based characteristics that have survival value for the plant in its home environment (Daubenmire 1974). Where intraspecific morphological variation is particularly distinct or consistent, a subspecies (ssp.) or variety (var.) may be designated. Taylor and MacBryde (1977) has been used as the standard reference for recognition of subspecific plant taxa in this publication.

Intraspecific variation may not be morphologically obvious. In fact, physiological adaptations to local environments are more common (Daubenmire 1974). Populations with distinctive adaptations for survival under local conditions are known as ecotypes. Very little is known about the ecotypic variation of most of the plant species included here, but it is clear that there are important autecological differences within most species found across many degrees of latitude and in several biogeoclimatic zones or subzones. For example, Holloway and Zasada (1979) observed that information from southern Canada and the central U.S. regarding the reproductive characteristics of plant species is often incorrect when applied to the same species in Alaska.

2.2 Distribution and Abundance

This section and the accompanying distribution map outline the geographical distribution in British Columbia of each plant species, and indicate its relative abundance in the various biogeoclimatic zones.

Information regarding the distribution of each species was obtained from published works (principally Hosie 1973; Hultén 1974; Krajina *et al.* 1982; Pojar *et al.* 1982; Angove and Bancroft 1983; and various B.C. Provincial Museum handbooks); from herbarium records on file at the B.C. Provincial Museum; and from discussions with vegetation researchers throughout the province.

In this publication the B.C. Ministry of Forests' ecosystem classification is used frequently to describe terrestrial ecosystems within the province. Readers not familiar with this classification system should refer to Pojar (editor, 1983) for background information. The abbreviations used throughout the text to refer to the biogeoclimatic zones are listed in Table 1.

2.2.1 Altitudinal range

Information regarding the altitudinal limits of plant species is scanty and comes primarily from Lyons (1952) for shrubs and herbs and Fowells (compiler, 1965) for tree species. There is a tendency for the species to have the broadest altitudinal distribution in the centre of their range, and to become confined to low elevations in the north and to higher elevations at the southern limits of their range.

TABLE 1. Abbreviations of biogeoclimatic zones

Abbreviation	Biogeoclimatic Zone
AT	Alpine Tundra Zone
BWBS	Boreal White and Black Spruce Zone
CCPH	Coastal Cedars – Pine – Hemlock Zone
CDF	Coastal Douglas-fir Zone
CWH	Coastal Western Hemlock Zone
ESSF	Engelmann Spruce – Subalpine Fir Zone
ICH	Interior Cedar – Hemlock Zone
IDF	Interior Douglas-fir Zone
MS	Montane Spruce Zone
MH	Mountain Hemlock Zone
PPBG	Ponderosa Pine – Bunchgrass Zone
SWB	Spruce – Willow – Birch Zone
SBS	Sub-Boreal Spruce Zone

Source: Pojar (editor) 1983.

2.3 Habitat

An important concept in the discussion of habitat is that of **ecological amplitude**, which refers to the range of habitat variation a species can endure (Daubenmire 1974). Species with a wide ecological amplitude are tolerant of a wide variety of environmental conditions, while species with a narrow ecological amplitude are highly specialized for a particular ecological niche.

Because of the effects of competition from other plants, the observed ecological range of a species may differ significantly from the range of habitats it is capable of occupying (Barbour *et al.* 1980). Similarly, the abundance or dominance of a species in a particular habitat does not necessarily indicate that the physical factors of that habitat are optimal for growth of the species. Many species apparently adapted to the "least favourable" habitats will, in the absence of competition, grow far better in "favourable" conditions and owe their ecological preference to low competitive ability and high tolerance of extremes (Fitter and Hay 1981).

2.3.1 Climatic relations

Climatic relations refer to the plant's adaptation to prevailing conditions of temperature, humidity, rainfall, snow, and wind. Most comments describe macroclimatic or regional climatic conditions, but as Daubenmire (1974) points out, microclimate is of more immediate concern in autecology since a plant responds to the environment that actually envelops it. The local environment may be considerably modified from the macroclimate by local topography and surrounding plant cover.

Detailed characterization of the climatic relations of individual plant species is lacking. The comments included in this section are largely subjective interpretations of the species' geographic and altitudinal distribution. No attempt has been made to quantify climatic conditions or to use any standardized climatic classification.

2.3.2 Site and soil conditions

Descriptive information about characteristic habitats is included in this category, along with details about landforms or parent materials, slopes, soil texture, and other soil profile characteristics.

2.3.3 Nutrient relations

Mineral nutrition is an important aspect of plant autecology because an adequate supply of certain mineral elements is essential for successful growth. Although relatively little intensive research has been done on the specific mineral requirements of native plant species, most research indicates that the basic requirements of native woody species are similar to those of intensively studied cultivated plants (Kramer and Kozlowski 1979). Nonetheless, there are large differences, both between and within species, in the ability of a plant to absorb and use mineral nutrients. Optimum pH levels also differ

between species that invade disturbed or young soils and those adapted to conditions in relatively undisturbed coniferous forest.

In the context of coniferous forest ecosystems, many deciduous species are regarded as site improvers (Fowells (compiler) 1965; West and Tueller 1972). Nutrient cycling within the ecosystem is enhanced by the rapid turnover of nutrients in deciduous foliage. The litter of deciduous species frequently contains higher concentrations of minerals and decays more rapidly than coniferous litter (Kramer and Kozlowski 1979). The higher pH of deciduous litter may also reduce leaching losses from the soil profile in certain situations (Valentine *et al.* (editors) 1978).

Of all the mineral elements, nitrogen probably is the most important. Nitrogen is frequently deficient in British Columbia forest soils (Freyman and van Ryswyk 1969; Hoyles 1979), and can be a major limitation to plant growth (Kramer and Kozlowski 1979). The nitrogen-fixing ability of alders can improve soil nutrient conditions (Tarrant and Miller 1963), and allows these species to invade heavily disturbed nitrogen-deficient soils (Viereck and Little 1972). Most of the species in this publication respond positively to additions of nitrogen, provided competition from other plants is not limiting (see, for example, Freyman and van Ryswyk 1969; Nelson 1974; Stanek *et al.* 1979).

2.3.4 Water relations

Moisture, more than any other single environmental factor, limits plant growth (Kozlowski 1972), and within an area of homogeneous climate, factors that affect moisture availability exert major control over the distribution of plant species in the landscape. In this section the range of moisture conditions over which the plant is typically found, its drought tolerance, and its tolerance of flooding are considered. Detailed studies of water relations are lacking for most of the plant species. The autecological importance of water is well documented in Daubenmire (1974) and Kramer and Kozlowski (1979).

2.3.5 Light relations

Light intensity, duration and quality are key determinants of plant vigour and also have regulatory effects on various aspects of a plant's life history (USDA 1974; Lavender 1981). The shade tolerance of species is discussed, although, as Krajina *et al.* (1982) caution, generalizations about shade tolerance that do not take into account ecosystem conditions and the different stages of a plant's life cycle rarely provide meaningful information. In the shade, most species become suppressed and wane, and few produce seeds; in full light they grow more rapidly, produce fuller foliage and usually produce abundant seed (USDA 1974). Photoperiod is instrumental in triggering many events in the plant's life cycle, particularly the onset of winter dormancy, but daylength also affects the amount of photosynthesis possible and thus directly affects plant growth rates (Lavender 1981).

The spectral quality of light in the shade differs from full sunlight because shorter wavelengths are less able to penetrate the overhead canopy than longer, near infra-red wavelengths. Differences in spectral quality affect many plant functions (Lavender 1981). Long-wave radiation can penetrate beneath litter and humus layers and inhibit the germination of buried seed (Kenady 1978).

2.3.6 Temperature relations

Discussion of temperature relations may include information about the optimal temperatures for plant growth, the importance of temperature and thermoperiod in triggering phenological events, and the tolerance of the plant to heat and cold temperatures or frost. However, temperature relations of all selected species, except red-osier dogwood, are poorly studied.

Both air and soil temperatures are ecologically important. Air temperatures in British Columbia are generally favourable to plant growth during late spring and summer, but soil temperatures at northern latitudes can severely restrict the potential for growth. Extremely high temperature at the soil surface can damage young plants (Lavender 1981), but such conditions are probably uncommon except in the southern Interior or on some south aspects.

Most species become dormant well in advance of cold winter temperatures, and once dormant they are basically immune to low temperatures (see, for example, Smithberg and Weiser 1968). Plants are most susceptible to frost damage early in the growing season and during flowering and fruit set (Sharp 1974; USDA 1974).

2.4 Growth and Development

The vegetative growth of above- and below-ground plant parts is considered in this section. Both morphological and physiological aspects of growth and development are significant, but technical aspects of plant physiology are beyond the scope of this report and there is little information on this subject for native plant species. Kramer and Kozlowski (1979) and Bidwell (1974) are good reference texts for basic information about the physiology of plant growth and development.

The life form of a plant (whether it is a tree, a tall or low shrub, or a herbaceous plant) has a major effect on its competitive abilities. Factors such as longevity, size and structure of stem and root systems, leaf form, leaf area, and leaf longevity determine how well the plant will compete for limited site resources with other plant species (West and Tueller 1972).

All of the species discussed in this publication are perennial species, with underground perennating organs (roots, rhizomes, etc.) that allow them to store reserves of energy through the dormant season, and permit rapid expansion of the foliage in spring (Grime 1979).

Many of the trees and taller shrubs compete successfully because their stature and long lifespan place them in the overstory, above smaller competitors. These species often have the added advantage of rapid juvenile height growth.

Many of the plants are also capable of lateral spread, by means of rhizomes, prostrate stems, or extensive horizontal root systems. This ability to develop clonal colonies with a high density of shoots and roots is a very effective means of occupying a site and pre-empting its resources (Grime 1979).

2.4.1 Phenology

Plant phenology refers to those periodic phenomena in the annual cycle of a plant that are controlled by climatic factors (Daubenmire 1974). Phenological events can be both morphological and physiological in nature and are controlled by predictable environmental factors such as photoperiod, temperature, summer drought, fall rains, and frost. In perennial plants, vegetative phenology includes such events as budbreak, leaf expansion, shoot growth, leaf senescence and leaf fall, bud set, and winter dormancy. Reproductive or flowering phenology includes flowering times, fruit ripening, flower bud initiation, and seed dispersal. Conard (1983) outlines important aspects of shrub phenology and the role that they can play in forest vegetation management.

The timing of phenological events is an important part of a plant's competitive strategy (Grime 1979). For example, some plants such as salmonberry take advantage of the mild coastal climate to leaf-out early and gain a maximum vegetative advantage over associated plant species (Barber 1976). Plants that rely on sexual reproduction may time flowering events such that successful pollination (Heinrich 1976) or early seedling establishment (e.g., *Populus* spp.) is ensured.

2.5 Reproduction

The reproductive strategy of a plant is of fundamental importance in plant autecology and forest vegetation management. Reproductive strategies include how a plant establishes itself on a site, how it increases in abundance following establishment, and how it persists through various stages of plant succession and habitat alteration.

2.5.1 Seed production and dispersal

This section describes (where available) the age of sexual maturity, the frequency and size of seed crops, the nature of the propagule (seed, fruit, or spore), and the method and efficiency of dispersal of each plant species.

Most species reviewed in this guide begin to produce seed between the ages of 2 and 10. Fruit and seed production rates are strongly affected by plant vigour, climatic factors, and biological agents. Most species disperse their seed from late summer to winter, although certain species have early-ripening seed.

Wind is an effective means of dispersal for light, small seeds, fruit, or spores. Seeds of other species are dispersed by gravity only. The seed of riparian species like willow and alder can be carried great distances by running water. Fleshy fruits are usually adapted for dispersal by birds and mammals (USDA 1974).

2.5.2 Seed viability and germination

Seed viability refers to both the germinative capacity of the seed and the length of time it can remain in a quiescent state before it loses its ability to germinate. The length of seed viability can vary from a few days to several decades or more. Many plants whose seeds remain viable for extended periods are known as "seed bankers" (Grime 1979; Rowe 1983). Seed of these species accumulates in the forest floor until environmental conditions become favourable for germination and subsequent plant growth.

The seeds of most North American plants are in a dormant state immediately following dispersal to prevent them from germinating too late in the year. The most typical form of seed dormancy is broken by several months of chilling (stratification) and the seeds germinate in the spring following dispersal (USDA 1974). Seeds that become ripe early in the growing season are usually capable of germination immediately following dispersal (see, for example, Fowells (compiler) 1965; Zasada *et al.* 1983).

Another form of seed dormancy is found in seeds with a very hard seed coat. These seeds require acid treatment or physical abrasion (scarification) to germinate. Seeds with seed coat dormancy are often found in species with fleshy fruit and some lose their dormancy after they pass through the digestive tracts of animals (Sharp 1974). Still other seeds may require exposure to high (fire-induced) temperatures to overcome dormancy (Rowe 1983).

The requirements for successful seed germination are adequate moisture, favourable temperatures, adequate gas exchange, and — for some species — light (USDA 1974). Most seeds will germinate on a variety of moist seedbeds, but moist mineral soil is preferred by many species. Seed germination requirements are normally much less critical than conditions required for successful seedling establishment (Fowells (compiler) 1965; Barber 1976).

There is great variance among the plant species included in this report in the relative importance of regeneration from seed. Some species like red alder reproduce almost entirely from seed, while for other species like trembling aspen, seedling production is an insignificant part of the reproductive strategy. Certain species, like bigleaf maple and oval-leaved blueberry, are "seedling bankers" (Grime 1979). Like western hemlock and amabilis fir, they produce advanced regeneration which can persist beneath a forest canopy for many years, but does not grow beyond the seedling stage until released from overstory shade.

2.5.3 Vegetative reproduction

All of the plants included in this report reproduce vegetatively in some form or another. Vegetative reproduction is the dominant form of regeneration in certain species, while other species merely replace damaged stems. Methods of natural vegetative reproduction include sprouting, suckering, layering, and rooting of stem or root fragments.

Sprouting is the dominant form of asexual reproduction. The term "sprouting" refers to production of new shoots from dormant or adventitious buds on stems or root collars.

Suckering refers to the production of new shoots from laterally spreading roots or rhizomes at some distance from the parent plant. Suckers tend eventually to become independent plants, thus leading to the production of genetically identical colonies or clones (Gill and Healy (compilers) 1974).

There is some disparity in the literature in the use of the terms sprouting and suckering. Many authors use suckering to describe the production of shoots from roots only, and refer to rhizome shoots as sprouts. The literature also includes a profusion of names for rhizome-like structures. Terms such as "rootstock", "underground stem", "stolon", and "runner" are variously used to describe prostrate branching structures that occur at or slightly beneath the soil surface and produce roots along their length.

Layering is a form of vegetative reproduction that takes place when straggling stems come in contact with the ground surface and produce roots. Eventually the branch may form a new plant.

Most perennial plants can be reproduced artificially from root or stem cuttings. The same situation can occur in nature if a plant is fragmented through disturbance and the fragment becomes buried in a favourable rooting medium.

2.6 Predation and Pests

This section briefly describes some animals that feed on the plant, and provides some information about disease and insect pests.

2.7 Effects on Crop Trees

Plant species that grow in association with coniferous crop trees may have both negative and positive effects on conifer growth. Competitive and beneficial effects are discussed separately in this section.

2.7.1 Competition

The species included in this report were selected because they are known or believed to have a significant negative impact on the growth of coniferous crop trees. This section describes what is known about the importance of the plant as a competitor in different regions of British Columbia, and the nature of its competitive interactions with coniferous crop trees. For most species there are few data documenting the nature and extent of competition.

The following list outlines some possible negative effects of competing vegetation on crop trees (Conard 1983, 1984):

1. Moisture competition. Competing vegetation normally results in a net loss of moisture from a site.
2. Shading. Overtopping vegetation reduces light available to crop trees.
3. Nutrient competition. Most perennial plants cause net depletion of nutrients in the soil profile.
4. Reduced soil and air temperatures. Shading and insulation of the forest floor by foliage and litter can reduce crop tree growth.
5. Allelopathy. Some plants release chemicals which interfere with the growth and development of crop trees.
6. Attraction of pests. Non-crop vegetation may provide shelter or supplementary food to rodents, browsing animals, or insect and diseases that damage conifer stands.
7. Mechanical damage. Seedlings may be compressed under snowpressed vegetation or damaged by wind-whipping.
8. Fire hazard. Shrubs and herbaceous vegetation may provide fuels that increase fire hazards.

2.7.2 Beneficial effects

Competing vegetation may also have a positive effect on the growth of crop trees in the short or long term. Aside from research into the nitrogen-fixing potential of alders, this topic has received little attention. Non-crop vegetation can potentially provide the following benefits to crop trees:

1. Increased relative humidity and soil moisture. Evapotranspirative stresses to the crop tree may be reduced through shading and transpiration by surrounding vegetation, and by the mulching effect of plant litter.
2. Reduced temperature extremes. Shade from surrounding vegetation may prevent damage from excessively high temperatures or frost.
3. Improved nutrient relations. Non-crop vegetation can act as a site improver through nitrogen fixation or through deposition of rapidly decomposing, nutrient-rich litter.
4. Reduced pest damage. Non-crop vegetation may act as an alternative food source, or discourage pests from entering conifer stands.
5. Reduced long-term competition. A cover of low-growing or short-lived plants may prevent the invasion of longer-lived, more aggressive competitors.

2.8 Response to Disturbance or Management

This section describes how each species is adapted to habitat alteration, and how cover, abundance, and plant vigour may be affected by natural disturbance or management practices.

2.8.1 Forest canopy removal

Literature describing how the plant species responds to partial or complete overstory removal through harvesting, thinning, or by natural means is summarized in this section. Most of the selected species respond favourably to the increased light following canopy removal by developing a fuller crown and increasing flower and fruit production, provided evapotranspirative stresses do not become extreme. Some species increase rapidly in abundance through vegetative spread or seeding-in.

2.8.2 Fire

The response of the competing species to natural or prescribed fire is discussed. Many of the species are adapted to environments where periodic fire is a natural event, and they may be favoured by fire (Wright 1972). Rowe (1983) gives a good summary of the adaptations of plants to fire. There are three main processes by which vegetative recovery takes place following fire: (1) sprouting or suckering from residual plant parts (usually underground structures) that have survived the fire, (2) germination of seed buried in the forest floor, and (3) invasion by wind- or animal-dispersed seeds and spores. McLean (1969) categorizes the relative fire resistance of herbaceous and shrub species according to the depth and structure of their roots and rhizomes.

The response of a plant to fire also depends on the severity of the fire. Fire severity or intensity is a function of weather, soil, and fuel conditions. The degree of damage to, or stimulation of, underground perennating organs and buried seed is usually directly related to fire intensity, as measured by the amount of surface organic material removed, and the depth of heat penetration into the soil (Miller 1977; Rowe 1983).

2.8.3 Cutting and grazing

Manual cutting of woody species is carried out either as a silvicultural treatment or to simulate the effects of browsing animals in wildlife studies. Herbaceous species may be subject to grazing, and a few species have been experimentally clipped to simulate grazing. The response of plants to cutting, browsing, or grazing depends on their ability to reproduce by means of sprouts or suckers and is a function of season, frequency or intensity, height and angle of cutting, and the age of the plant (Gill and Healy (compilers) 1974; Harrington 1984; Hoyer and Belz 1984). Light browsing or single cutting treatments will merely stimulate growth of most sprouting or suckering species; however, repeated cuttings will eventually exhaust the carbohydrate reserves of all but the most resistant plants.

2.8.4 Herbicides

This section summarizes reports of herbicide applications to the selected species. The emphasis is on chemicals registered for forestry use in British Columbia, and, where possible, on studies conducted in British Columbia. No attempt has been made here to provide detailed descriptions of the conditions under which the herbicides were applied, or of the response of the plant. Because of the large number of variables affecting plant sensitivity and herbicide efficacy (Newton and Knight 1981), it is recommended that readers consult the referenced articles for specific details.

2.8.5 Soil disturbance

This section summarizes the plant's known or expected response to natural or man-caused soil disturbance. Most of the information available describes the plant's ability to colonize disturbed areas through germination of buried or newly deposited seed, or to regenerate from root and stem fragments. There is little information regarding the effects of mechanical site preparation techniques used in silviculture on individual plant species. Studies of the plant's response to agricultural treatments can provide useful information.

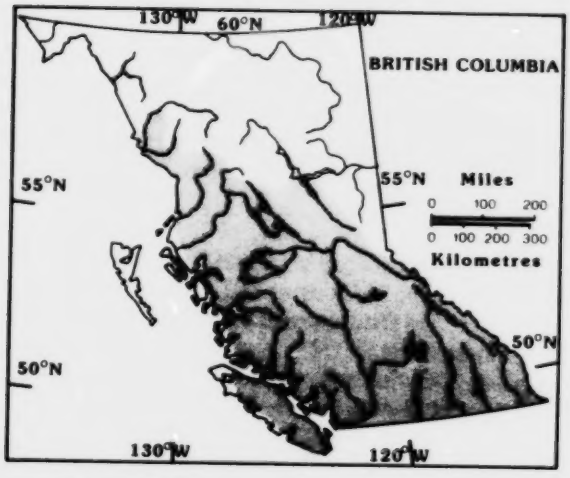
2.8.6 Fertilization

Nitrogen fertilizers applied to the plant species under discussion generally improve vigour, growth rates, and fruit production (see, for example, Freyman and van Ryswyk 1969; Nelson 1974); however, the plants vary in their ability to respond to additions of other essential elements (Nelson 1974; Watt 1976).

Fertilizers applied to improve the growth of crop trees may cause the vigour and cover of competing species to increase as well (Turner 1979). Increased vigour and shading of overstory trees may partially offset this response (Stanek *et al.* 1979).

3 AUTECOLOGICAL CHARACTERISTICS OF SELECTED PLANT SPECIES

Acer glabrum (Douglas maple).



Distribution of *A. glabrum* in British Columbia.

Acer glabrum Torr. **Douglas maple**
(Rocky Mountain maple)

DESCRIPTION

Douglas maple is a deciduous small tree or shrub. It reaches 6–9 m in height and up to 30 cm in diameter but most often occurs as a multistemmed shrub 1.5–2 m tall. Stems are red with opposite branching; leaves are palmate with three- to five-toothed lobes, often reddish tinged. The imperfect flowers are small, greenish yellow in drooping clusters. Male and female flowers can occur on separate trees. Fruit are paired, winged samaras, wrinkled, green to red in colour but becoming greyish brown with age (Viereck and Little 1972; Hosie 1973; Hultén 1974).

Variation: The Douglas maple of British Columbia is variety *douglasii* (Taylor and MacBryde 1977). Studies done in the United States refer to the Rocky Mountain maple (*Acer glabrum* var. *glabrum*) (Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Douglas maple is found throughout most of B.C. to approximately 56°N latitude. It is uncommon on the outer Coast and absent from the Queen Charlotte Islands (Viereck and Little 1972; Krajina *et al.* 1982). It is most abundant in the Interior of the province, especially in southern B.C., in the IDF and drier ICH subzones.

Altitudinal Range: Although most common in Interior valley bottoms, Douglas maple grows from sea level to over 1200 m (Lyons 1952). It is generally absent from subalpine elevations.

HABITAT

Climatic Relations: Within B.C., Douglas maple does not appear to tolerate climatic extremes, as it is absent from areas of extremely wet coastal climate, from the boreal forest, from the semi-desert areas of the southern Interior, and from alpine and subalpine climates. Throughout central B.C. it appears to prefer areas of moist, warm mesoclimate (R. Coupé, pers. comm., Nov. 1984) and is characteristically found on sunny south-facing slopes (Coupé *et al.* (compilers) 1982; Coupé and Yee (editors);[1] C. Delong, unpublished data, 1983, B.C. Min. For., Prince George, B.C.). In northern Idaho, Mueggler (1965) found that *A. glabrum* was more abundant on south aspects, but Cline and Campbell (1976) cite it as a species that occurs equally on north and south aspects.

Site and Soil Conditions: In the mature forest of the SBS, northern ICH and drier CWH subzones, Douglas maple is characteristically found on well drained colluvium or on shallow soils (Coupé and Yee (editors);[2] Yole *et al.*;[3] C. Delong, unpublished data, 1983, B.C. Min. For., Prince George, B.C.). In the IDF and southern ICH, and in seral communities throughout B.C. it occurs on a much wider range of sites and soils (see e.g., Mitchell and Green 1981). Along the Coast, Douglas maple is commonly found on rocky cliffs, ledges, and avalanche tracks, or bordering openings such as meadows and bogs (Viereck and Little 1972; Hosie 1973). It is also abundant on alluvial terraces of coastal river valleys (J. Pojar, pers. comm., March 1985).

Nutrient Relations: *Acer glabrum* is believed to have relatively high nutritional requirements. Krajina *et al.* (1982) state that it has high requirements for calcium, magnesium, nitrogen, potassium, and phosphorus, while Mueggler (1965) reports that it is associated with sites having high levels of potassium.

Moisture Relations: Throughout B.C., Douglas maple grows over a wide range of moisture conditions. It tends to be most common on dry sites in wet biogeoclimatic zones (CWH and ICH), and on moister sites in drier zones such as the IDF (Angove and Bancroft 1983), but its best growth occurs on moist coastal bottomlands where it can become a medium-sized tree. Cline and Campbell (1976) studied the water relations of *A. glabrum* in northern Idaho where it was present on both moist, north aspects and dry, south aspects. During August, when evapotranspirative stresses were much higher on the south aspect, the south aspect maple had maximum conductances which were almost twice as high as those on the north aspect. The maple is

[1] R. Coupé and A.R. Yee (editors). 1982. Identification and interpretation of ecosystems of the Cariboo Forest Region (EP 822.04). B.C. Min. For., Williams Lake, B.C. Unpublished draft.

[2] Coupé and Yee (editors), 1982.

[3] D. Yole, J. Pojar, and B. Robinson. 1982. Ecosystem classification of the Coastal Western Hemlock Zone within the Mid Coast Timber Supply Area, Prince Rupert Forest Region, British Columbia. B.C. Min. For., Smithers, B.C. Unpublished report.

apparently able to compete on both sites by adjusting its total leaf area, through stomatal control, and by shifting the water potential of its leaves on the south aspect to enable it to extract the less available soil moisture.

Light Relations: Krajina *et al.* (1982) classify Douglas maple as having moderate shade tolerance. It occurs in relatively open forest and under full sunlight, but rarely in deep shade. It has been found at 4% of full light levels in the forests of southern Oregon (Emmingham 1972). Strong sunlight can be detrimental to young seedlings (Marchant and Sherlock 1984). Mueggler (1965) observed that it is a tall spindly shrub under a canopy, and a more dense, compact shrub in open sunlight.

Temperature Relations: Frost resistance is classified as high, especially in the Interior, by Krajina *et al.* (1982).

GROWTH AND DEVELOPMENT

There is no detailed information available on the morphological or physiological development of *A. glabrum*. The species appears to develop more often as a single stemmed tree in the favourable environments of coastal and southern B.C., where on moist productive sites it can attain heights of 10 m or more. In the Interior and on harsh coastal sites it is usually seen as a multistemmed shrub (Hosie 1973; USDA 1974). Seedlings are large and will grow rapidly during the first growing season if conditions are favourable (Marchant and Sherlock 1984). Maximum height growth is ordinarily attained within 30 to 40 years of establishment (Mueggler 1965). It has a wide-spreading root system with a mixture of deep and lateral roots (Hosie 1973; Marchant and Sherlock 1984).

Phenology: Flowering occurs between April and June. In coastal Alaska flowering typically occurs in May and fruit maturation takes place in July and August, while in Montana and Idaho flowers open between mid-May and mid-June and fruit ripening extends from mid-July into September. Seeds are dispersed beginning in September and can remain on the stems until February or later (Viereck and Little 1972; USDA 1974; Schmidt and Lotan 1980; Shaw 1984).

In Montana and Idaho, leaf emergence can begin in early April and is complete by late May. Leaves are fully grown by mid-June at most locations. They begin to colour and die between late July and early September, depending on weather conditions, and leaf fall extends from early September to mid-October (Cline and Campbell 1976; Schmidt and Lotan 1980).

REPRODUCTION

Seed Production and Dispersal: Douglas maple begins to produce seed from an early age (USDA 1974). Crane *et al.* (1983) report that seeds were produced by the 5th year following a fire. There is a 1- to 3-year interval between large seed crops (USDA 1974). The winged seeds are dispersed throughout the fall and winter by wind (USDA 1974) and there are no reports of dispersal by animals.

Seed Viability and Germination: Douglas maple seeds remain viable for only a short period of time. Seeds remaining on the stem may slowly lose their viability during dry, frosty periods (Marchant and Sherlock 1984). Under ideal conditions seed can be stored for up to 3 years. High germination percentages (e.g., 85%) have been obtained under laboratory conditions. The seeds have embryo dormancy and require approximately 180 days of chilling before they will germinate (Shaw 1984).

Vegetative Reproduction: Douglas maple sprouts readily from root crowns following disturbance (Cholewa and Johnson 1983; Crane *et al.* 1983), but does not appear to spread by rhizomes or root suckers. Vigorous natural layering has been observed in the mountain maple *(Acer spicatum)* of eastern North America (Hosier 1974).

PREDATION AND PESTS

Acer glabrum is a preferred browse species of wildlife (Asherin 1974; Cholewa and Johnson 1983).

EFFECTS ON CROP TREES

Competition: Douglas maple is not considered to be a significant competitor with conifers over most of its range (Krajina *et al.* 1982; R. Coupé, and C. Delong, pers. comm., Nov. 1984). In the Kamloops Forest Region, however, it is viewed as a major competitor (D. Lloyd, pers. comm., Nov. 1984). There are no studies of its competitive ability, but it is usually not an aggressive colonizer of clearcuts, and because it has a relatively open crown, it does not cause serious competition for light. Competition with conifers for moisture seems

likely in the dry climate of the IDF, and on dry sites in other subzones. Because of its apparent nutrient-demanding status, it may also compete successfully with conifers for soil nutrients.

Beneficial Effects: Krajina *et al.* (1982) indicate that the litter of this species has a beneficial effect on humus, presumably because of the rapid recycling and decomposition of the high concentrations of nutrients contained in maple foliage. C. Delong (pers. comm., Nov. 1984) has suggested that it may be beneficial to leave maple to provide shade for Douglas-fir on some harsh sites. However, the benefit of shade may be offset by competition for moisture on these sites.

RESPONSE TO DISTURBANCE OR MANAGEMENT

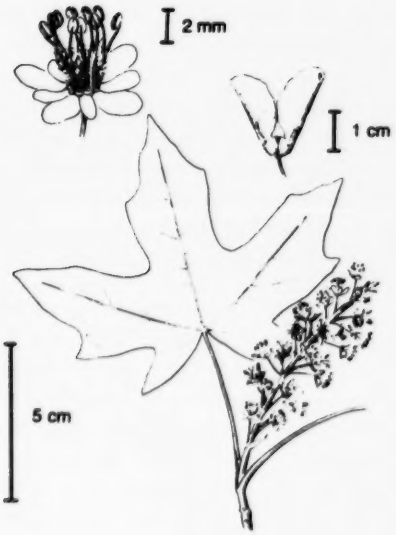
Forest Canopy Removal: Successional studies in the cedar-hemlock zone of northern Idaho (Mueggler 1965; Wittinger *et al.* 1977) indicate that the cover of *A. glabrum* increases slightly or not at all following canopy removal, and begins to decline 25 years following canopy removal. The form of the maple shrub becomes broader and foliage becomes more dense following canopy removal. Eis (1981) showed a significant increase in cover of *A. glabrum* 6 years following logging on moist *Aralia-Dryopteris* sites in the SBS zone north of Prince George but did not indicate whether the increase was due to establishment of new seedlings or an increase in vigour of existing plants.

Fire: Several authors report that *A. glabrum* sprouts readily from the root crown following fire and increases in density because single plants produce multiple sprouts (Lyon 1966; Cholewa and Johnson 1983). Crane *et al.* (1983) observed that resprouting occurred the same year as the fire and 5 years later, maple had increased 4 times over its original post-fire cover. Stickney (1981), however, reports that *A. glabrum* is fire sensitive; survival was low and percent cover remained well below preburn levels after 9 years. Differences in observed results may relate to fire intensity.

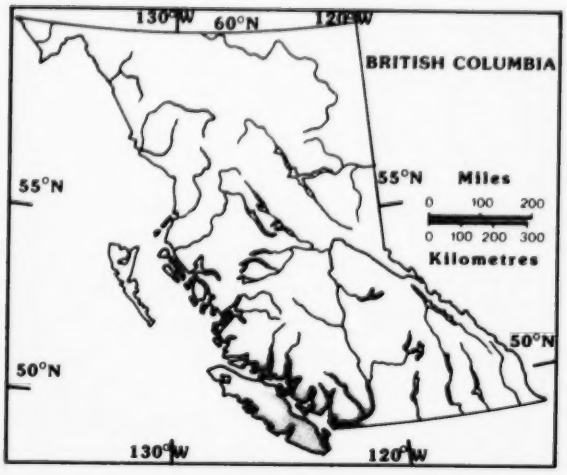
Cutting: Resprouting following cutting is similar to burning response (Marchant and Sherlock 1984).

Herbicides: There is very little information concerning the chemical control of *A. glabrum*. M. Newton (pers. comm., Dec. 1984) has found that, in Oregon, glyphosate applied in the fall at 1.7 kg/ha provides good control, whereas 2,4-D usually results in defoliation or top-kill followed by sprouting.

Soil Disturbance: No information.



Acer macrophyllum (bigleaf maple).



Distribution of *A. macrophyllum* in British Columbia.

Acer macrophyllum Pursh. — Bigleaf maple (broadleaf maple)

DESCRIPTION

Bigleaf maple is a large tree 15–25 m tall at maturity, with a broad, spreading crown. Twigs are stout with opposite branching. Leaves are large (15–30 cm) and palmate with deep lobes. The yellowish green flowers are arranged in a raceme at the ends of the twigs. The fruit is a winged samara with paired, hairy seeds (Hosie 1973; Brand[4]).

Variation: There are no varieties or subspecies of bigleaf maple described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Bigleaf maple in B.C. is confined to Vancouver Island and the adjacent mainland coast as far north as Sullivan Bay (Hosie 1973; Krajina *et al.* 1982). It penetrates inland up the Fraser Canyon to Lytton. It is found only in the CDF, CWH, and subcontinental IDF biogeoclimatic zones, and is most abundant on southeastern Vancouver Island and adjacent areas of the CDF zone.

Altitudinal Range: A low-elevation species, bigleaf maple rarely occurs above 300 m (Fowells (compiler) 1965), but has been observed at elevations above 350 m on southeastern Vancouver Island (Packee 1976).

HABITAT

Climatic Relations: Bigleaf maple is confined to the warmest, mildest climate found in B.C. (Krajina *et al.* 1982). The northern limit of the species is apparently restricted by temperature, while insufficient moisture and humidity may combine with temperature to limit its extension towards the Interior. Its best growth occurs in a humid climate where mean annual temperatures are above 10°C and there is little annual variation in temperature (Fowells (compiler) 1965).

Site and Soil Conditions: Bigleaf maple is found on a variety of soils ranging from deep and loamy to shallow and rocky. Best growth is found on fluvial sites and at the base of colluvial slopes (Fowells (compiler) 1965; Packee 1976), but it may also be found on morainal and marine soils, and often appears as pioneering vegetation following landslides. Hosie (1973) reports that it occurs most often on coarse, gravelly soils. Soils supporting good growth of bigleaf maple are most often classified as Humo-Ferric Podzols, Sombric or Dystric Brunisols, and Regosols (see e.g., Klinka *et al.* 1979; Klinka and Carter 1980).

Nutrient Relations: Best growth of bigleaf maple occurs in nutrient-rich soils, and it has very high requirements for calcium, magnesium, nitrates, potassium, and phosphorus (Krajina *et al.* 1982). Levels of nitrogen, potassium and calcium in foliage, wood, bark, and litter are high relative to other northwestern tree species, while levels of phosphorus and magnesium are relatively low (Minore 1979).

Water Relations: Bigleaf maple most often grows where soils are moist, and best growth is on sites with abundant seepage or on fluvial sites along streambanks (Fowells (compiler) 1965; Hosie 1973; Packee 1976; Krajina *et al.* 1982). Minore (1979) classed *A. macrophyllum* as intermediate relative to other Pacific Coast tree species with respect to optimum moisture conditions. Its flood tolerance is rated as very high by Krajina *et al.* (1982) who observe that it occurs on floodplains.

Light Relations: In B.C., bigleaf maple is not normally found as an understory tree.[5] Shade tolerance is described as low to moderate (Krajina *et al.* 1982). However, it is the most shade-tolerant deciduous tree in south coastal B.C. (Packee 1976). Current research in coastal Oregon (J. Tappeiner, pers. comm., Dec. 1984) indicates that young seedlings are sufficiently shade tolerant to develop under young conifer stands, but tolerance seems to decrease with age, and best growth occurs where top light is available (Fowells (compiler) 1965).

Temperature Relations: The geographic distribution of bigleaf maple suggests that frost resistance is low, and that the species cannot tolerate frozen soil conditions (Krajina *et al.* 1982).

[4] D.G. Brand. 1984. Assessment of the growth of Douglas-fir plantations. IV. Characteristics and dynamics of competing vegetation. University of B.C., Vancouver, B.C. Unpublished report.

[5] Ibid.

GROWTH AND DEVELOPMENT

Bigleaf maple is characterized by rapid growth for the first 40–60 years of its life. Maturity is reached at between 150 and 300 years of age and mature trees reportedly average about 15 m tall and 45 cm in diameter (Fowells (compiler) 1965), but trees may be more than 30 m tall and as much as 2.5 m in diameter. Under low light conditions, bigleaf maple develops a narrow crown and a long limb-free bole. Under open grown conditions its crown is broad and rounded (Hosie 1973). The tree has a wide-spreading root system (Packee 1976).

This species is most often seen in cutovers as a multistemmed clump arising from a cut stump rather than as an individual of seed origin.[6] Sprouts and seedlings of bigleaf maple have quite different juvenile growth characteristics (M. Newton, pers. comm., Dec. 1984). Sprouts can grow 2-4 m in height in the first growing season. Their height growth is controlled by the number of sprouts and the size of the original stump. Within 30 to 40 years the clump can cover an area as large as 100 m^2 (Lauterbach and Warren 1982; Brand;[7] Roberts[8]). In contrast, early seedling growth is much slower because the seedling does not have an established root system and large carbohydrate reserves. Seedlings established under a canopy of other species may have extremely slow rates of growth until released by removal of the overstory (J. Tappeiner, pers. comm., Dec. 1984). Suppressed trees are extremely persistent and can die back and resprout repeatedly under overmature conifer stands (M. Newton, pers. comm., Dec. 1984).

Phenology: Flowers and leaves emerge simultaneously from the same bud during April. Pollination occurs 2–4 weeks following bud burst. Fruits ripen between late August and October and are dispersed from October through January (Fowells (compiler) 1965; Hosie 1973; USDA 1974). In a western Oregon study, the peak period of leaf abscission was 2–23 October. Abscission occurred rapidly following the first frost and was hastened by heavy rains (Campbell and Franklin 1979).

REPRODUCTION

Seed Production and Dispersal: Bigleaf maple first begins to produce flowers at about 10 years of age. Pollination of the flowers is by insects. Seed crops are produced every year and can be copious. Open grown trees begin to produce seed earlier in life and have larger seed crops than those growing in the shade. Seeds are dispersed throughout the fall and winter. Dispersal is primarily by wind but small mammals and some birds may also be involved. The seed is one of the heaviest of northwestern tree species, but the large wings aid in effective dispersal (Fowells (compiler) 1965; Minore 1979).

Seed Viability and Germination: The seed has a very short period of viability and cannot be stored at low or room temperature even for short periods of time (USDA 1974). Germination apparently occurs on both mineral and organic seedbeds and survival depends on the presence of adequate moisture (Packee 1976).

Vegetative Reproduction: Bigleaf maple sprouts vigorously from dormant buds at the base of the stem following top-kill or cutting of the parent tree (Fowells (compiler) 1965; Brand[9]; Pendl and D'Anjou[10]). It does not produce suckers from rhizomes or roots and there are no reports of natural layering.

Reproductive Strategy: Researchers in Oregon, studying the establishment of bigleaf maple hypothesize that it is a "seedling banker" (v. Grime 1979). This regenerative strategy involves a bank of persistent seedlings that establish themselves under young coniferous or mixed stands, then persist in a stunted or etiolated condition until a disturbance occurs that creates conditions favourable for more rapid growth (J. Tappeiner, pers. comm., Dec. 1984). Seedlings of bigleaf maple are rarely found in Oregon clearcuts; however, there is some uncertainty whether this failure to become established is due to environmental conditions or whether deer browse of young seedlings is so severe that seedlings only become established at later stages of stand development when deer are less abundant (M. Newton, pers. comm., Dec. 1984).

PREDATION AND PESTS

As noted above, seedlings and saplings are favoured by black-tailed deer. Maple seeds are also eaten by many small mammals and some birds (Fowells (compiler) 1965). Principal diseases and insect pests are

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[6] Brand, 1984.

[7] Ibid.

[8] C. Roberts. 1980. Second year report — Cooperative brush control study. (Project co-ordinated with Oreg. State University, Forestry Research Laboratory), Corvallis, Oreg. Unpublished report.

[9] Brand, 1984.

[10] F. Pendl and B. D'Anjou. 1984. Operational trial of the herbicide "Roundup" at Pender Harbour. Establishment Report. B.C. Min. For., Vancouver, B.C. Unpublished report.

described by Fowells (compiler, 1965), Packee (1976), and Furniss and Carolin (1977). Minore (1979) rates *A. macrophyllum* as being particularly resistant to laminated root rot *(Phellinus weirii).*

EFFECTS ON CROP TREES

Competition: Bigleaf maple is considered to be a very serious and pernicious competitor with Douglas-fir on some of the most productive growing sites in B.C. It does not aggressively seed-in to clearcut sites (D. Minore, pers. comm., Dec. 1984), thus the primary source of competition is from plants already established on the site, especially those trees cut during logging. Bigleaf maple sprouts easily outgrow B.C. conifers and because a single plant has the capacity to establish cover over a large area, the potential stocking by desired species is greatly reduced.[11] No other individual of any plant species provides as much competition to Douglas-fir as a single sprouted stump of bigleaf maple (M. Newton, pers. comm., Dec. 1984). Its large leaves produce a deep shade that does not allow shade-intolerant species such as Douglas-fir to become established (Krajina *et al.* 1982), and the heavy leaf fall also smothers young seedlings (Packee 1976). Bigleaf maple is often outgrown in height by conifers (Fowells (compiler) 1965), but this does not occur until relatively late in the rotation.

Beneficial Effects: Although bigleaf maple absorbs and retains large quantities of nutrients, its litter is believed to be valuable in providing a rich supply of nutrients to a site. The mull humus, which develops where maple litter is deposited, is apparently beneficial to western redcedar (Krajina *et al.* 1982).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Plants already established on the site can be expected to respond to canopy removal with vigorous growth. Cut stumps sprout to produce a wide-crowned multistemmed shrub. Rapid seeding-in of cutover areas is not observed in coastal Oregon (D. Minore and J. Tappeiner, pers. comm., Dec. 1984). In a coastal B.C. study (Mueller-Dombois 1965), spread of bigleaf maple tended to be confined to moist, nutrient-rich sites similar to those where the maple is normally found in mature forest.

Fire: Burning produces top-kill of bigleaf maple followed by rapid sprouting from dormant basal buds. Sprouts can grow 3–4 m per year (Kelpsas 1978; B.M. Geisler, pers. comm., Jan. 1985). A severe prescribed burn completely eliminated bigleaf maple for at least five growing seasons on a site in the western Cascades of Oregon. Light burning produced no significant difference in cover from preburn conditions (Dyrness 1973).

Cutting: When sprouted maple clumps were manually cut back with axes, the coppices regrew almost immediately.[12] Bigleaf maple cut during three different seasons averaged six sprouts per cut stem with the least sprout production occurring on the late summer cuttings.[13]

Herbicides: Selective broadcast applications of most available herbicides will cause top-kill but roots are seldom killed because little chemical is transported downwards. The plant quickly responds by producing sprouts (Sund and Finnis 1978; Lauterbach and Warren 1982). Stem injection or treatment of exposed cambium on freshly cut stumps with triclopyr appears to successfully prevent most sprouting (Sund and Finnis 1978; M. Newton, pers. comm., Dec. 1984). Glyphosate is also effective if injected in the fall, and picloram is moderately effective.

Soil Disturbance: Large crawler tractors and backhoes were used to uproot stumps of bigleaf maple on Vancouver Island. Stump sprouting was minimal and sprouts were of very low vigour (B.M. Geisler, pers. comm., March 1985).

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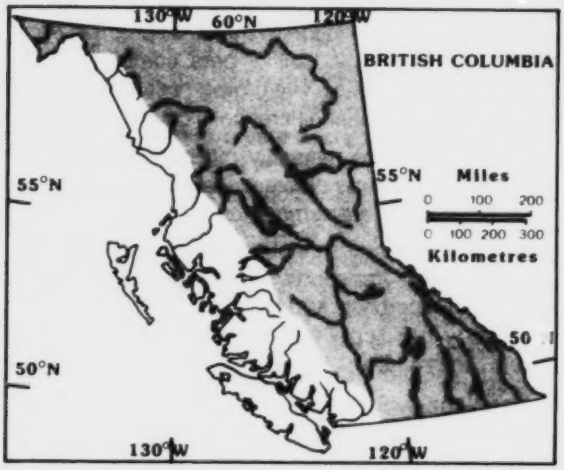
[11] Brand, 1984.

[12] Pendl and D'Anjou, 1984.

[13] Roberts, 1980.

Alnus incana ssp. *tenuifolia* (mountain alder).



Distribution of *A. incana* ssp. *tenuifolia* in British Columbia.

***Alnus incana* (L.) Moench**
spp. *tenuifolia* (Nutt.) Breit.
(A. tenuifolia)

Mountain alder
(thin-leaved alder, speckled alder)

DESCRIPTION

Mountain alder is a deciduous small tree or coarse, multistemmed shrub up to 15 m tall. Stems have smooth greyish yellow bark and twigs have club-shaped stalked buds. Leaves are thin, oval, non-sticky, with teeth quite noticeably of two sizes. Separate male and female catkins are produced on the same twig. Fruits are small nutlets with tiny wings, and are borne in cones (Hosie 1973; Brayshaw 1978; Furlow 1979).

Variation: Mountain alder is very closely related to the speckled alder (*A. incana* ssp. *rugosa* or *A. rugosa*) of the prairie provinces and eastern Canada, and to the grey alder (*A. incana* ssp. *incana*) of Europe. Several varieties of this subspecies have been described, but they are poorly distinguished because the morphological variation is continuous rather than discrete (Hosie 1973; Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Mountain alder is found throughout British Columbia east of the Coast Mountain Range. It occurs widely in all Interior biogeoclimatic zones, but is only locally abundant (Hosie 1973; Taylor and MacBryde 1977; Krajina *et al.* 1982; Angove and Bancroft 1983).

Altitudinal Range: Mountain alder ranges from 100 m in Alaska to over 3000 m in Colorado and Arizona (Furlow 1979). In B.C., it ranges from Interior valley bottoms to high mountain elevations (Lyons 1952), but does not extend as high as Sitka alder (J. Pojar, pers. comm., March 1985).

HABITAT

Climatic Relations: *A. incana* requires cool climatic conditions throughout its range (Furlow 1979). The range of this species in B.C. indicates that it is adapted to a wide variety of continental climatic conditions and can tolerate a broad range of temperature and precipitation.

Site and Soil Conditions: Mountain alder is most often associated with alluvial or streambank habitats (Hultén 1974; Brayshaw 1978). In Great Britain, *A. incana* is known for its ability to thrive on very cold, heavy soils (Hadfield 1968).

Nutrient Relations: The nutritional requirements of mountain alder are high. It is described as a calciphyte by Krajina *et al.*(1982) and is usually found growing in moderately rich to rich habitats (Pojar *et al.* 1982; R. Coupé, pers. comm., Nov. 1984). Wali (1969) found that near Prince George, mountain alder is restricted to a very narrow range of site conditions with high rates of available calcium, magnesium, and nitrogen. Like other alders, mountain alder has the capacity to fix atmospheric nitrogen (Fleschner *et al.* 1976). It fixes higher rates of nitrogen than Sitka alder and can produce amounts similar to red alder (Binkley 1981). On floodplain sites in Alaska, soil pH gradually decreased under a stand of mountain alder over a period of 20 years and there was a marked increase in potassium, calcium, magnesium, manganese, and phosphorus within 5 years of mountain alder establishment (Van Cleve and Viereck 1972).

Water Relations: Throughout B.C., mountain alder is most common on wet sites (C. Delong, R. Coupé, W.R. Mitchell, and D. Lloyd, pers. comm., Nov. 1984) and it seems to have higher moisture requirements than *A. viridis*. Flood tolerance is high (Krajina *et al.* 1982), but Knighton (1981) found that growth and root development of speckled alder (*A. incana* ssp. *rugosa*), which is also abundant on saturated soils, were severely reduced when water levels were at or above the root crown.

Light Relations: Mountain alder is quite shade-tolerant (Krajina *et al.* 1982) and is frequently found growing in the shade of the understory. However, it is usually found where there is good exposure to sunlight (Lyons 1952). Sprouts may be more tolerant of shade than seedlings (Healy and Gill 1974).

Temperature Relations: Mountain alder has a high tolerance of frost (Krajina *et al.* 1982). In Europe, *A. incana* is able to thrive in areas subject to late and early frosts (Hadfield 1968).

GROWTH AND DEVELOPMENT

Mountain alder is usually a large shrub or small tree with multiple stems, similar in appearance to green and Sitka alder, but frequently taller and straighter (C. Delong, pers. comm., Nov. 1984). Under favourable conditions

it can produce a single trunk with a diameter up to 25 cm and a height of 15 m (Hosie 1973; Furlow 1979). At high elevations it often becomes a scraggly, sprawling shrub (Lyons 1952). It frequently forms pure dense clumps in wet pockets and along streams.

Mountain alder is much less aggressive, in terms of its growth rate and its ability to invade new territory, than red alder and the European grey alder (*A. incana*) (Krajina *et al.* 1982).

Phenology: Male and female catkins of mountain alder expand before the leaves in spring. Flowering occurs during March and April in the northwestern U.S. and during May and June in the interior of Alaska. The cones ripen in late fall with seedfall occurring immediately following ripening. Leaves remain green until they drop in fall (Lyons 1952; Viereck and Little 1972; USDA 1974; Brayshaw 1978).

REPRODUCTION

Seed Production and Dispersal: Mountain alder produces abundant seed. The fruit is a small, single-seeded nutlet with a narrow wing. Disperal is by wind and water (Hosie 1973; USDA 1974).

Seed Viability and Germination: Seed viability can be low: in some cases as many as 95% of seeds produced have been found to be empty. The seed requires no treatment or chilling to break dormancy and can be expected to germinate immediately following dispersal if conditions are favourable (USDA 1974). In eastern North America, speckled alder requires saturated soil for seed germination, and seed is the primary source of new stands on freshly exposed, wet soil (Healy and Gill 1974).

Vegetative Reproduction: Like other alders, mountain alder can sprout from the root collar or stump if damaged. Both the European grey alder and the eastern speckled alder are reported to produce suckers at some distance from the main stem (Hadfield 1968; Healy and Gill 1974). Sprouting from exposed roots in streams has been noted, and submerged branches sometimes produce adventitious roots (Furlow 1979). Layering has also been reported in some alders and could be possible in mountain alder considering its sprawling branches and moist habitat. Cuttings of *A. incana* taken in Alaska could not be successfully rooted (Holloway and Zasada 1979).

Although this species frequently occurs in thickets, it is not known whether such groups of plants represent clones (Furlow 1979). Healy and Gill (1974) believe that in eastern North America, perpetuation and spread of established alder stands probably result mostly from sprouting or other vegetative means.

PREDATION AND PESTS

Alder seeds, buds, and catkins are eaten by many birds, and large and small mammals will feed on twigs and foliage (Healy and Gill 1974). However, as a browse species, its preference by most predators is low.

In B.C., common insect pests include the alder flea beetle *(Altica ambiens)* and the striped alder sawfly *(Hemichroa crocea)*, the western tent caterpillar *(Malacosoma californicum)*, and the poplar-and-willow borer *(Cyrptorhynchus lapathi)* (Gerber *et al.* 1980).

EFFECTS ON CROP TREES

Competition: On wet sites, mountain alder often forms dense thickets that compete severely with conifers, preventing natural regeneration or successful establishment. Scattered individual trees usually do not pose a significant threat to planted conifers.

Beneficial Effects: An important beneficial effect of mountain alder is its ability to improve soil nitrogen status. *A. incana* can fix between 43 and 360 kg/ha of nitrogen annually (Binkley 1981). The beneficial effect of nitrogen fixation on the growth of associated conifers should be most evident on nitrogen-deficient sites (Harrington and Deal 1982). Mountain alder may improve nutrient availability on forest sites (see e.g., Van Cleve and Viereck 1972). In Britain, grey alder has been used as a nurse crop, interplanted with shade-tolerant trees like *Thuja plicata* on microsites that were too wet and frost prone for the young conifers (Hadfield 1968).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Most published references to the response of *A. incana* to disturbance or management refer to spp. *rugosa* (e.g. Healy and Gill 1974)

Forest Canopy Removal: *A. incana* increases in abundance after harvesting, especially on wet sites (Healy and Gill 1974; C. Delong and W.R. Mitchell, pers. comm., Nov. 1984). In Alaska, density increased following summer and winter logging of an alluvial balsam poplar stand; increases were greatest on winter logged areas (Zasada *et al.* 1981).

Fire: Where alders are present but suppressed, fire will tend to favour the alder over competing species (Healy and Gill 1974).

Cutting: Spring and winter cutting produces rapid sprout growth, while cutting in July and August produces fewer, slower-growing sprouts. Alder retains its vigour and sprouts heavily when subjected to repeated cutting at 4- to 5-year intervals (Healy and Gill 1974).

Herbicides: No information.

Soil disturbance: Mechanical treatments that expose areas of wet mineral soil will provide a suitable seedbed for mountain alder. Sprouting can be expected from root crowns and stem bases of alders damaged during mechanical site preparation. In the Cariboo Forest Region, trials using a V-plow or straight blade to rip apart large areas of alder have apparently been successful in setting back the alder sufficiently to establish a softwood crop.[14]

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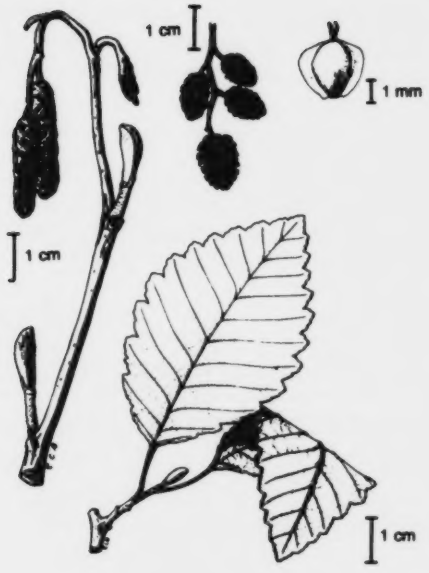
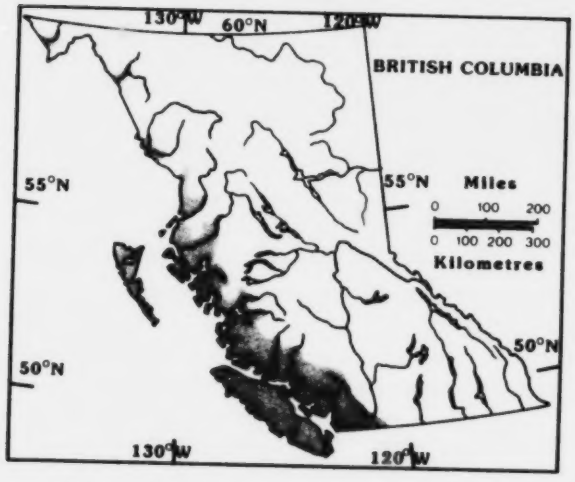
[14] J. Perry. 1983. Hardwood invasion on cutblocks in the Cariboo Forest Region. B.C. Min. For., Williams Lake, B.C. Unpublished report.



Alnus rubra (red alder).



Distribution of *A. rubra* in British Columbia.

Alnus rubra Bong. — Red alder

DESCRIPTION

Red alder is a medium-sized deciduous tree up to 25 m tall. Stems have smooth grey bark, twigs are reddish with club-shaped stalked buds. Leaves are oval, doubly toothed with an in-rolled margin. Separate male and female catkins are produced on the same plants. The female catkins develop into small cones containing small, winged nutlets (Brayshaw 1978).

Variation: No subspecies or geographic varieties are decribed in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Red alder is the most abundant hardwood occurring along the northwest Pacific Coast. In B.C. it is found along the entire length of the coast, including Vancouver Island and the Queen Charlotte Islands. It is restricted to within 200 km of the coast and only occurs inland of the Coast Mountains along major river valleys such as the Fraser and Skeena (Fowells (compiler) 1965). Red alder is abundant in the CWH, CCPH, and CDF zones and is found at low elevations in the MH.

Altitudinal Range: Red alder is primarily a species of low coastal valleys, ranging from sea level to approximately 800 m (Fowells (compiler) 1965).

HABITAT

Climatic Relations: Red alder grows in humid to perhumid coastal climates with annual precipitation ranging from 400 to 5600 mm. Most of the precipitation within its range occurs as rain during the winter. The range of red alder appears to be limited at northern latitudes and inland by low winter temperatures (Fowells (compiler) 1965), but the factors controlling its distribution are not well understood. Plants transported to Michigan, where the winters are quite severe, proved to be perfectly hardy (Furlow 1979).

Site and Soil Conditions: Red alder is found on a wide variety of soils and substrates ranging from well-drained gravels and sands, to poorly drained clays or organic soils. The best stands are found on deep, well-drained loams or sandy loams of alluvial origin (Fowells (compiler) 1965). Red alder has been found to increase soil bulk density over time (Bormann and Debell 1981).

Nutrient Relations: Red alder has a major influence on the nutrient conditions of a site. It is well known for its ability to increase soil nitrogen through its symbiotic association with nitrogen-fixing bacteria and for its contributions to the organic matter content of a soil (Tarrant and Miller 1963; Binkley 1981; Bormann and Debell 1981). Nitrogen accretion rates are variable and depend on factors such as stand location, vigour, composition, age, density, and the inherent fertility of the site (Debell *et al.* 1983). Accretion rates ranging from 45 to 335 kg/ha per year have been reported for red alder stands up to 50 years old (Burns (compiler) 1983).

Red alder also affects soil nutrient status in other ways. As soil nitrogen increases in soils under an alder stand, there is a drop in soil pH and a concurrent decrease in exchangeable calcium and magnesium. Foliar concentrations of several nutrients, especially phosphorus, have been found to decrease with stand age. A similar decrease in the phosphorus content of leaf litter has also been observed (Bormann and Debell 1981; Debell *et al.* 1983, 1984).

The relationships decribed above suggest that the growth of red alder may be limited by the natural levels of phosphorus, calcium, or magnesium in the soil (Debell *et al.* 1984), especially in light of its high nutritional requirements for these nutrients (Krajina *et al.* 1982).

Water Relations: Red alder tolerates poorly drained soil conditions and survives prolonged periods of flooding (Krajina *et al.* 1982). Among its associates, it is considered to be one of the most tolerant species of shallow water tables (Minore 1979). It is found on a wide range of soil moisture conditions (Krajina *et al.* 1982), but is uncommon on droughty soils or in areas of low precipitation and it seldom occurs on steep south or southwest-facing slopes where it may be subject to severe evapotranspirative stresses (Fowells (compiler) 1965).

Light Relations: Red alder has low shade tolerance (Krajina *et al.* 1982) and does not occur as an understory plant except on wet, productive sites where the mature forest has a very open canopy.[15] Establishment and subsequent growth is best in full sunlight.

Temperature Relations: Frost resistance of red alder is low (Krajina *et al.* 1982).

GROWTH AND DEVELOPMENT (Fowells (compiler) 1965; Hosie 1973; C. Harrington, unpublished data, U.S. Dep. Agric. For. Serv., Olympia, Wash. 1981)

Red alder exhibits rapid early growth. Of its associates, only black cottonwood and bigleaf maple sprouts can grow as rapidly during the juvenile stage. Where moisture is adequate, a seedling can grow to 1 m or more in the 1st year. Maximum annual height growth of over 3 m a year can be achieved by 2- to 5-year-old seedlings. It is possible for a seedling to be nearly 10 m tall by age 5.

Growth slows after the juvenile stage, with the decrease beginning much earlier on poor sites. Red alder is a short-lived tree, becoming decadent at 40 years, and rarely living for more than 60 years.

In most situations red alder grows as a single-stemmed tree; multistemmed shrubs are rare. Under low light conditions the crown is narrow, but in full light in the absence of competition, branches spread out from near the base to produce a broad, rounded crown.

Growth and yield of red alder are described in detail in Briggs *et al.* (1978).

Phenology: Red alder flowers between late February and early May depending on latitude and climate (Kenady 1978). In coastal Alaska, flowering is in April and May (Viereck and Little 1972). Cone ripening takes place between August and September. Seed dispersal begins shortly after ripening and continues through fall and winter (Kenady 1978).

REPRODUCTION

Seed Production and Dispersal: Red alder begins to produce seed at about 6–8 years of age with optimum production occurring at about age 25. It produces ample seed every year with bumper crops every 3 to 5 years. Dissemination of seeds is primarily by wind. The narrowly winged nutlets can be carried great distances (Fowells (compiler) 1965; USDA 1974; Kenady 1978; Burns (compiler) 1983).

Seed Viability and Germination: Red alder seed remains viable in storage for at least 3 years. There is very little difference in germination percentage between stratified and unstratified seed. Seed germinates best after a period of water imbibition. Germination in nature is best on moist mineral soil in full sunlight. Far-red light that penetrates through thick layers of vegetation or surficial soil layers strongly inhibits seed germination. This prevents seed from germinating until after a disturbance, when it is exposed to full sunlight. Red alder will germinate on decayed wood and litter but survival of seedlings is best on mineral soil. Seedlings can tolerate partial shade for several years but full sun is required for normal development (Fowells (compiler) 1965; Kenady 1978). Germination of seed on freshly exposed mineral soil is the primary method of regeneration in red alder.

Vegetative Reproduction: Red alder sprouts vigorously from the root collar or stump when young. Once alder reaches age 15 its capacity for vegetative reproduction is greatly diminished, and few trees will produce sprouts that live for more than 2 years (Debell *et al.* 1984). Red alder does not sucker from the roots (Harrington 1984). Greenwood cuttings from young trees can be successfully rooted (Monaco *et al.* 1980). Vegetative reproduction allows recovery of individual damaged trees, but is not a means of population growth in this species.

PREDATION AND PESTS

Red alder is exceptionally free from disease and other damaging agents for the first 40 years (Fowells (compiler) 1965). For more detailed information on the pests of red alder refer to Fowells (compiler, 1965), Gerber *et al.* (1980), and Burns (compiler, 1983).

[15] Brand, 1984.

EFFECTS ON CROP TREES

Competition: Red alder is a major competitor with young conifer plantations thoughout its range in B.C. Seedlings that establish in disturbed areas following logging form the primary source of competition. Sprouts that develop from stems cut during logging are a lesser source of competition for young trees.

Most studies on the effect of alder competition on crop trees have involved Douglas-fir. Alder competition reduces height, diameter, and biomass of Douglas-fir (Cole 1984), and can cause significant mortality (Miller and Murray 1978).

The rapid juvenile growth of red alder gives it a competitive advantage over Douglas-fir, and competition becomes more pronounced with time as the growth of alder outstrips that of Douglas-fir. Without chemical or mechanical control, equal-aged alder usually overtops associated Douglas-fir for about the first 25 years (Miller and Murray 1978). Newton *et al.* (1968) concluded Douglas-fir needs 4–9 years of free growth prior to alder encroachment to ensure successful regeneration.

Alder canopies allow considerable penetration of light, and they tend to suppress moderately shade-tolerant conifers like Sitka spruce, rather than kill them outright (Brand;[16] authors' personal observation). Alder competition also involves many factors other than light. Competition for soil moisture is certain to be a factor on many sites, and Debell *et al.* (1983, 1984) have shown that available nutrients are decreased under a canopy of red alder. Del Moral and Cates (1971) found that extracts of red alder foliage and litter inhibited growth of test plants in the laboratory, but there was no evidence that allelopathic interference was occurring under field conditions.

Beneficial Effects: The primary beneficial effect of red alder on the growth of crop trees is its ability to increase the nitrogen content of forest soils. Red alder interplanted with Douglas-fir clearly increased height and diameter growth of the associated dominant conifers on a nitrogen-deficient site in southwestern Washington (Miller and Murray 1978). The authors recommended that 50–100 uniformly distributed alders per hectare be retained for nitrogen improvements. Benefits should be greatest on soils that are deficient in total or available nitrogen and low in organic matter and clay (Miller and Murray 1978; Binkley 1982). Red alder also increases soil organic matter content (Tarrant and Miller 1963; Bormann and Debell 1981).

Another potential beneficial effect of red alder in mixtures with conifers may be its ability to reduce losses from laminated root rot (Nelson *et al.* 1978).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Red alder will rapidly invade clearcut areas if a seed source is available, especially if disturbance has created areas of exposed mineral soil (Hosie 1973; Kenady 1978).

Fire: Red alder is generally one of the first trees to become established on burned-over areas (Hosie 1973). Fire is rarely a damaging agent to established pure stands of red alder because of their extremely low flammability; in fact, red alder has been planted to act as a firebreak to protect adjacent conifers (Fowells (compiler) 1965).

Cutting: Red alder will sprout from the stem following cutting, but it is not considered a strong sprouter compared with other species. Coppicing experiments have shown the effects of tree age, cutting height, cutting angle, season of cut, and repeated cuttings on the sprouting vigour of red alder (Debell *et al.* 1984; Harrington 1984; Hoyer and Belz 1984). The major findings of these studies are as follows:

1. Sprouting vigour is greatest on trees aged 1–3 years. Vigour falls off dramatically after 15 years. Trees aged 15 years or older rarely have live sprouts 2 years after cutting.
2. The average number of sprouts per cut stem increases significantly as stump height is increased (e.g., five sprouts on stumps below 10 cm; nine on 70-cm stumps).
3. Stumps with the cut surface facing south or west have the least mortality and are most likely to sprout, presumably because of light interception. Level cuts have higher mortality and fewer sprouts than angled stumps, possibly because water is slower to drain off, causing faster decay.
4. Stems cut in January had the lowest mortality; stems cut during the growing season, especially in July or August, had the greatest mortality.
5. The number of sprouts per cut stem is not affected by the season of cutting.

[16] Brand, 1984.

6. Trees cut for the first time in January at age 2, and every 2nd year for 8 years thereafter, showed a significant reduction in sprouting vigour after every cut.

In a Vancouver Island study, 5-year-old alder were cut in September. After the first growing season, there were 3 to 6 times as many stems as prior to treatment, and sprouts were up to 2 m tall. By the end of the second growing season, alder competition was equal to or greater than it was prior to treatment.[17]

Herbicides: Red alder is very sensitive to 2,4-D (Stewart 1974*a*, 1974*b*; Conard and Emmingham 1984*a*, 1984 *b*). Timing of foliar applications of 2,4-D is not critical (Stewart 1974*a*). The response of red alder to foliar sprays of glyphosate has been variable, and ranges from moderate (25–60%) to very severe (90–100%) injury (Conard and Emmingham 1984*a*, 1984*b*). Spring through fall basal sprays using glyphosate cause very severe damage to red alder (Conard and Emmingham 1984*b*). Red alder is very sensitive to applications of triclopyr (Conard and Emmingham 1984*a*).

Soil Disturbance: Red alder readily seeds in to areas of exposed, moist mineral soil (Fowells (compiler) 1965). Scarified sites in the Vancouver Forest Region had a much higher cover of red alder than unscarified and burned sites.[18] Dense stands of red alder are almost invariably associated with soil disturbances such as roads, landings, and other forms of localized deep scarification (Newton *et al.* 1968).

Fertilization: Growth of young red alder may be substantially enhanced by applications of non-nitrogenous fertilizers. Phosphorus fertilizers produced the greatest response, but alder also responded to applications of calcium, magnesium, potassium, and sulphur in greenhouse and field studies (Debell *et al.* 1984).

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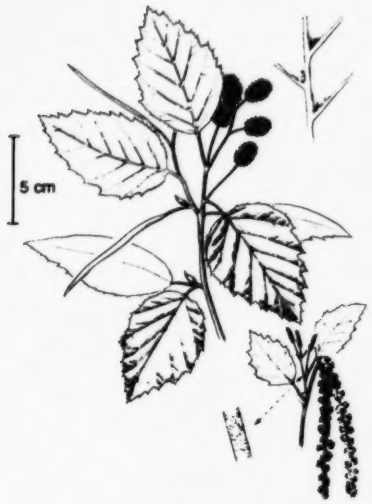
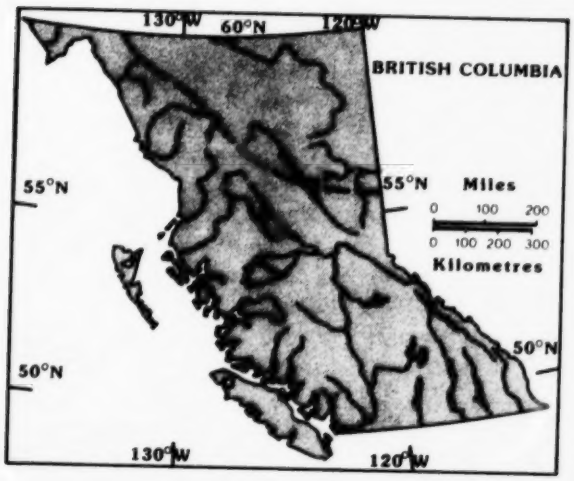
[17] B.G. Dunsworth. 1985. Northwest Bay operational brush control trial. Progress report 1984/1985. MacMillan Bloedel Ltd., Nanaimo, B.C. Unpublished report.

[18] Brand, 1984.



Alnus viridis ssp. *sinuata* (Sitka alder).



Distribution of *A. viridis* in British Columbia. Subspecies *fruticosa* (green alder) is dominant north and east of the dashed line, while ssp. *sinuata* (Sitka alder) dominates to the south and west. There is a broad area of introgression between the two subspecies.

Alnus viridis* ssp. *sinuata **Sitka alder**
(*A. sinuata, A. sitchensis, A. crispa* ssp. *sinuata*) (slide alder)

Alnus viridis* ssp. *fruticosa **Green alder**
(*A. viridis, A. crispa* ssp. *crispa*)

These two alders are very similar, although their exact taxonomic relationship and designation may be in dispute. They are discussed together here to avoid repetition. Most of the available literature applies to Sitka alder. Information provided on Sitka alder can probably be applied to green alder as long as allowances are made for the latter's boreal habitat.

DESCRIPTION

Sitka and green alder are deciduous shrubs or small trees up to 7–10 m tall. Bark is yellowish brown, and twigs have pointed, sessile axillary buds. Leaves are ovate to elliptic, with sharp serrations and shallow lobes, sticky beneath when young. Separate male and female catkins are born in small clusters on the same twig. The cone-shaped female catkins have slender stalks and produce small, wide-winged nutlets (Brayshaw 1978; Furlow 1979; Harrington and Deal 1982).

Variation: Green and Sitka alder are known by a variety of scientific names. They are closely related and interbreed freely, producing intermediate forms where their ranges overlap in northern British Columbia (Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Sitka alder ranges from the Alaska border south through B.C. and eastward to the Rocky Mountains (Hosie 1973). It is found throughout the province except northeast of the Rocky Mountains where it is replaced by green alder. There is no area of the province where one of the two subspecies cannot be found (Brayshaw 1978; Krajina *et al.* 1982). Green alder is virtually restricted to the BWBS and SWB zones while Sitka alder is found in every biogeoclimatic zone except the PPBG (Krajina *et al.* 1982; Angove and Bancroft 1983).

Altitudinal Range: Sitka alder is a species predominantly of middle to higher forested elevations in B.C. It has been found from 100 m to 1500 m on Vancouver Island (Binkley 1981), but Harrington and Deal (1982) were unable to find any below 500 m in Washington state. It is often found near the upper timberline in the mountains of B.C. (Brayshaw 1978) and forms a subalpine to alpine scrub in northwestern B.C. (J. Pojar, pers. comm., March 1985). Green alder is found from valley bottoms to timberline elevations in northeastern B.C.

HABITAT

Climatic Relations: Both Sitka and green alder are cold climate species. While green alder is clearly adapted to the harsh, boreal climate, Sitka alder is found in cool, moist situations and shady aspects at both high and low elevations within its range (Mueggler 1965; Hosie 1973; Tiedemann and Klock 1974). The springy branches of Sitka alder allow it to tolerate heavy snow loads and sustain only minor damage during avalanches (Lyons 1952; Marchant and Sherlock 1984).

Site and Soil Conditions: Sitka alder is well known as a colonizer of disturbed soils, appearing on avalanche tracks, talus slopes, fresh alluvium, and behind retreating glaciers, but it may also be found in relatively stable environments within the forest and along streams. It is found on a wide variety of parent materials and soil textures (Johnson 1968; Mitchell 1968; Viereck and Little 1972; Furlow 1979). Green alder is found on a similar variety of habitats within its range (Brayshaw 1978; Krajina *et al.* 1982; Foote 1983), but is most often associated with sandy, gravelly, or rocky soil (Furlow 1979).

Nutrient Relations: The nutrient requirements of Sitka and green alder are high for calcium, magnesium, phosphorus, and potassium (Krajina *et al.* 1982), but growth is generally independent of the levels of nitrogen available on a site (Harrington and Deal 1982). Both alders are efficient nitrogen fixers (Crocker and Major 1955; Dalton and Naylor 1975; Carpenter *et al.* 1979; Binkley 1981). Reported rates of nitrogen fixation range from 20 to 62 kg/ha per year. Both alders fix less nitrogen than *A. incana* ssp. *tenuifolia;* Sitka alder, depending on age, produces approximately the same as or less nitrogen than *A. rubra* (Binkley 1981, 1982b; Heilman and Ekuan 1982). The ability of Sitka alder to fix nitrogen allows it to invade sterile mineral

soil that has been recently exposed by glaciers or avalanches and is very deficient in organic materials (Viereck and Little 1972; Krajina *et al.* 1982). Like red alder, it increases the soil nitrogen level and and builds up the organic matter content of young soils. Both Sitka and green alder appear to have an acidifying effect on soil. Crocker and Major (1955) observed that recently deglaciated soils under green alder were reduced from a pH of 8.0 to pH 5.0 within 35–50 years. Mitchell (1968) found some of the lowest soil pH levels (as low as pH 3.3) under Sitka alder in Alaska.

Water Relations: Sitka alder prefers cool, moist sites that are reasonably well drained. Unlike mountain alder, it is found on sites ranging from submesic to (sub)hygric in moisture status and is not abundant on very wet sites with a high water table (Pojar *et al.* 1982; Angove and Bancroft 1983). Similarly, Furlow (1979) notes that green alder is adapted to somewhat drier conditions than most alders, but still is usually associated with some source of moisture. Krajina *et al.* (1982) report that both Sitka and green alder have high resistance to flooding damage. Cline and Campbell (1976) describe Sitka alder in northern Idaho as a species that is poorly adapted to drought. It is absent from exposed, sunny sites because it lacks the physiological adaptations that are needed to prevent moisture loss from the foliage.

Light Relations: The shade tolerance of Sitka and green alder is described as moderate by Krajina *et al.* (1982). Both subspecies are able to grow as shrubs in the understory of taller tree species and are abundant in seral forest (Johnson 1978; Foote 1983; Pojar *et al.* 1984) but thrive on overhead light and are unable to withstand the shading of a dense coniferous overstory (Viereck and Little 1972).

Temperature Relations: Both Sitka and green alder are very tolerant of frost. Krajina *et al.* (1982) note that green alder is susceptible to frost damage if not covered by snow, but Foote (1983) reports that in Alaska, it is abundant on sites with very cold soil temperatures where the frost level is only 30 cm below the soil surface in midsummer.

GROWTH AND DEVELOPMENT

Alnus viridis is usually a large shrub or small tree with multiple stems. Growth rates vary considerably with site and location. Sitka alder on mild coastal sites grows much faster and taller than that growing in the Interior. In western Washington, height growth of Sitka alder slows rapidly on poor sites, but on better sites it can continue to grow at a steady rate for at least 10 years. It takes approximately 3–4 years to reach 1 m in height and can reach 4 m by age 10 (Harrington and Deal 1982). In central B.C. near Vanderhoof, Sitka alder typically reaches a mature height of only 3 m (C. Delong, pers. comm., Nov. 1984). Elevation also affects height growth, with decreased growth occurring at higher elevations (Hultén 1974; Harrington and Deal 1982). Sitka alder frequently develops crooked, upward curving limbs as a result of snowpress at higher elevations (Lyons 1952).

The growth of green alder is similar to that of Sitka alder except that it is smaller and slower growing, rarely developing into a small tree (Viereck and Little 1972; Brayshaw 1978). Three-year-old green alder seedlings reached a maximum height of 47 cm in Alaska (Zasada *et al.* 1983).

Phenology: Male and female catkins emerge before or with the leaves in spring. Flowering takes place in May and June in Alaska. Nitrogen fixation on the south Coast begins in May, concurrently with leaf emergence, and peaks in July. The cones ripen from mid-September to mid-November, dependent on latitude and elevation, and seed dispersal occurs immediately thereafter (Viereck and Little 1972; Brayshaw 1978; Binkley 1981; Marchant and Sherlock 1984).

REPRODUCTION

Seed Production and Dispersal: Sitka alder produces abundant seed that can be dispersed over long distances by wind or water (USDA 1974).

Seed Viability and Germination: Zasada *et al.* (1983) found 40% viable seed in a sample of green alder seed from Alaska. There is no information on the viability of Sitka alder seed after storage. The seed does not tolerate drying out (Zasada *et al.* 1983). A lengthy period of chilling is recommended for best germination (Marchant and Sherlock 1984). Sitka alder requires a moist mineral soil seedbed for germination (Viereck and Little 1972). Green alder germination begins early in the spring following dispersal and the majority of germination is complete by the end of June (Zasada *et al.* 1983). Germination from seed on disturbed habitats is the primary form of reproduction of both green and Sitka alder.

Vegetative Reproduction: Both green and Sitka alder sprout from the stump if damaged or cut. Sprouting from exposed roots in streams has also been noted in Sitka alder (Furlow 1979). This alder is not readily established from rooted cuttings (Marchant and Sherlock 1984). Vegetative reproduction may be important for the persistence of individuals between periods of disturbance but is generally insignificant as a means of reproduction of new plants and invasion of new areas.

PREDATION AND PESTS

These alders have relatively low browse value, although they are browsed somewhat by deer (Marchant and Sherlock 1984). Cones, buds, and seeds are eaten by birds (Healy and Gill 1974). Gerber *et al.* (1980) report that the alder flea beetle (*Altica ambiens*), the western tent caterpillar (*Malacosoma californicum*), and the poplar-and-willow borer (*Chrytorhynchus lapathi*) are common insect pests in B.C.

EFFECTS ON CROP TREES

Competition: Sitka alder is not considered as serious a brush problem as red alder on the south Coast because of its relatively slow growth rate and bushy habit (Binkley 1981, 1982a; Harrington and Deal 1982). In moist Interior areas, Sitka or green alder are often well established in the understory prior to harvest and can be a major competitor following harvesting (M. Tanner, pers. comm., Jan. 1985). Where scattered individuals occur on a cutblock they do not appear to constitute a major obstacle to plantation establishment (C. Delong, pers. comm., Nov. 1984), but they can form dense thickets—particularly on avalanche tracks in mountainous areas—that prevent conifer establishment over fairly large tracts of land.

Beneficial Effects: The major beneficial effect of these alders for crop trees relates to their ability to increase the nitrogen content of forest soils. Viereck and Little (1972) indicate that alder acts as a nurse tree to Sitka spruce on sterile sites, improving soil conditions and adding organic matter and nitrogen (see Crocker and Major 1955). The growth characteristics of Sitka alder make it a more desirable species for interplanting with conifers than red alder (Binkley 1981, 1982*b*; Harrington and Deal 1982). Sitka alder appears to beneficially affect Douglas-fir growth only on very nitrogen-deficient sites; Douglas-fir did not react positively to Sitka alder on fertile sites (Binkley 1982*a*). Harrington and Deal (1982) suggest that Douglas-fir should be established prior to interplanting with alder to ensure that the conifer is not suppressed. Sitka alder is also a valuable species for slope stabilization and erosion control on steep slopes (Marchant and Sherlock 1984).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Six years after harvesting, alder cover had remained constant or increased slightly from preharvesting levels, on four different site types in the SBS zone near Prince George (Eis 1981). Increases after logging have also been observed in the SBS zone near Vanderhoof and Fort St. James (J. Pojar, pers. comm., March 1985). Near Edson, Alberta, green alder had a lower cover 6–12 years following logging than under the mature forest canopy (Corns and LaRoi 1976).

Fire: Mueggler (1965) found that broadcast burning favoured Sitka alder in the cedar-hemlock zone of northern Idaho. Frequency and cover were especially increased on sites that had been repeatedly burned over a 30-year period. In the SBS of the Prince Rupert Forest Region, *A. viridis* is also abundant in areas with a history of frequent fires (Pojar *et al.* 1984). The authors speculate that the nitrogen-fixing alder may have been favoured over other invading species by severe fires that removed much of the surface organic matter and volatilized the soil nitrogen. Mitchell (1968) also reports that Sitka alder is an important factor on burned-over sites in Alaska.

Although alder invasion and persistence may be favoured by fire, established plants are relatively slow to recover from burning. In cool, wet subzones of the Kamloops Forest Region, Sitka alder reportedly takes 5–7 years to recover from broadcast burns of moderate to severe intensity (M. Tanner, pers. comm., Jan. 1985).

Cutting: Sitka and green alder are known to sprout following cutting (Marchant and Sherlock 1984), but there are no studies of their sprouting behaviour.

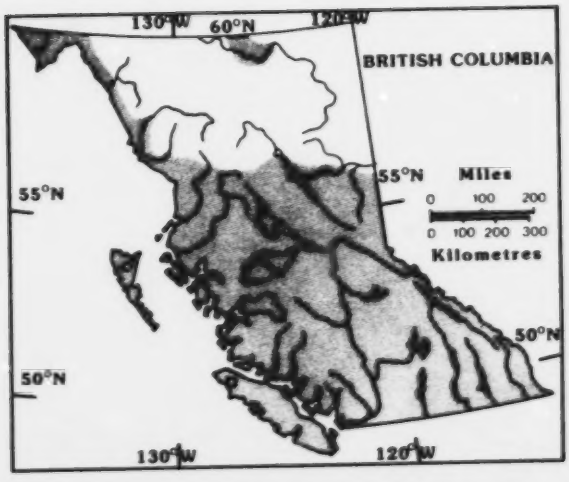
Herbicides: Sitka alder appears to be moderately susceptible to glyphosate.[19]

[19] R.J. Whitehead, J.R. Gilmour, and G.C. Ackerman. 1982. Blue River herbicide trial final report. SX79601Q. B.C. Min. For., Victoria, B.C. Unpublished report.

Soil Disturbance: Both Sitka and green alder are adapted to invade areas of exposed mineral soil by seed. They are often found colonizing areas of sterile, recently disturbed soil such as avalanches, recently exposed glacial deposits, and skid trails on logged sites (Johnson 1968; Viereck and Little 1972; G. Lloyd, pers. comm., Jan. 1985). Sprouting can be expected from root crowns and stem bases of alders damaged during mechanical site preparation. In the Cariboo Forest Region, trials using V-plows or straight blades to rip apart large clumps of alder have apparently been successful in setting back the alder sufficiently to establish a softwood crop.[20]

[20] Perry, 1983.

Athyrium filix-femina (lady fern).



Distribution of *A. filix-femina* in British Columbia.

Athyrium filix-femina (L.) Roth — Lady fern

DESCRIPTION

Lady fern has erect to spreading deciduous fronds up to 2 m tall arising from a stout, erect or ascending rhizome clothed in brown scales. The frond has a rather succulent bipinnate blade that tapers at both ends, and a short, scaly, stipe (stem) that is prone to breaking or bending. Spores are produced on the underside of the blade in oblong to horseshoe-shaped sori (Taylor 1973*a*).

Variation: Lady fern is a variable species of near world-wide distribution (Taylor 1973*a*). There are many geographical varieties of the species: the British Columbia version of this fern is described as ssp. *cyclosorum* (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Athyrium filix-femina can be found throughout most of B.C. wherever conditions are suitable for its growth (Taylor 1973*a*). It has not been collected from northeastern B.C. except for a location on the Liard River (A. Češka, pers. comm., Nov. 1984). Lady fern is one of the most common ferns in British Columbia. It occurs in all of the biogeoclimatic zones but is most abundant in the wet CWH and ICH zones and the SBSf subzone. It is extremely uncommon in dry areas of the southern and central Interior such as the PPBG zone and driest subzones of the IDF and SBS (Angove and Bancroft 1983).

Altitudinal Range: Lady fern ranges from sea level to subalpine and lower alpine elevations, to approximately 1200 m (Lyons 1952).

HABITAT

Climatic Relations: The distribution of lady fern in B.C. and elsewhere indicates that it can tolerate a broad range of temperature conditions, although it is mostly absent from the extremely cold boreal zone. Its absence from the driest Interior areas of the province suggests that it requires generally humid conditions during the growing season. In Britain, Page (1982) observes that it is most abundant in areas of high rainfall frequency and little summer drought. Mueggler (1965) found that the species was significantly associated with north aspects in the cedar-hemlock forests of northern Idaho, and this association with cool, humid habitats within its range is also typical in B.C.

Site and Soil Conditions: Lady fern is found in riparian and floodplain habitats, in rock crevices and on a variety of moist to wet soils in forests and meadows. It is also able to colonize a wide range of open, man-made, semi-natural situations. Soils are often Gleysols or gleyed subgroups of other soils (Campbell and Franklin 1979; Comeau *et al.* 1982; Coupé *et al.* 1982; Page 1982).

Nutrient Relations: In B.C., lady fern grows on sites with a wide range of available nutrients, but is most often found, on sites that are classified as medium rich (mesotrophic) to very rich (eutrophic) (see e.g., Klinka 1977*b;* Pojar *et al.* 1982; Utzig *et al.*[21]). However, Page (1982) describes it as "a calcifuge species, that avoids base-rich soils, except where these are overlain by acidic surface horizons". Wali (1969) found that in the SBS zone near Prince George, *A. filix- femina* occurred on sites with a wide range of available calcium and slightly higher than average levels of available nitrogen.

Water Relations: Lady fern grows in moist to wet soils. It occurs mostly in soils with good drainage, but which are kept permanently moist (Page 1982). In areas of dry climate it is restricted to hygric sites with abundant seepage, or to floodplains, but in areas of moister climate it occupies a broader range of moisture regimes. In very wet subzones of the Interior Wet Belt (e.g. ICHb, ICHh, SBSf, ESSFb, and ESSFh), it can be found on moisture regimes ranging from submesic to hydric (Comeau *et al.* 1982; Delong *et al.*[22]), presumably because there is sufficient moisture available to satisfy its high water requirements even on rapidly or well drained sites.

Light Relations: Lady fern has the ability to tolerate deep shade, but its best growth occurs in open woods or meadows where abundant sunlight and adequate moisture are available simultaneously. In shaded condi-

[21] G. Utzig, D. MacDonald, G. Still, M. Ketcheson, T. Braumandl, and A. Warner. 1963. Ecological classification for the Nelson Forest District. Third approximation. B.C. Min. For., Nelson, B.C. Unpublished report.

[22] C. Delong, S. Jenvey, and A. McLeod. 1984. A field guide for the identification and interpretation of ecosystems of the SBSf in the Prince George Forest Region. First approximation. B.C. Min. For., Prince George, B.C. Unpublished field manual.

tions, the lady fern blade is fairly flat, but with increasing light, the pinnae (leaflets) become angled downwards (Page 1982). This appears to be an adaptation enabling the plant to optimize light interception in low light, and reduce evapotranspirative losses in full sunlight. In a laboratory experiment (Zimmer 1976), lady fern grew continuously and showed no apparent difference in growth rate under a wide variety of photoperiods. Warm white light from fluorescent tubes produced better growth than narrower spectrum light from mercury tubes.

Temperature Relations: The dormant buds require at least 30 days of chilling between November and February in order for budbreak to occur the following spring (Hill 1976). The minimum temperature for vegetative growth is near 5°C. Between 10 and 20°C, temperature does not significantly affect the rate of growth (Zimmer 1976). Lady fern fronds appear to be very sensitive to frost.

GROWTH AND DEVELOPMENT

Ferns have a well-developed vascular system with true roots, stems, and leaves; however, ferns have no flowers, and their life cycle differs significantly from that of flowering plants (Keeton 1972). The germinating spore develops into a tiny cluster of undifferentiated cells known as a prothallus that bears male and/or female reproductive organs. The prothallus depends on an adequate supply of moisture for growth because it has no vascular system. Free water is also essential during this stage of the fern's life cycle to ensure fertilization of the eggs by free-swimming sperm. The fertilized egg develops into the large, leafy spore-bearing plant (sporophyte). The lady fern sporophyte is a perennial plant in which most or all of the fronds die back each fall and persistence is by means of a fleshy underground rhizome. Most moderate-sized fern sporophytes take from 1 to 5 years to reach maturity and produce spores (Page 1979). At maturity, the lady fern frond averages between 30 and 150 cm in length and 10 and 30 cm in width, but can reach a height of 2 m.

Lady fern often exists in the forest understory as small individual plants; however, when it is large and vigorous it is most often found in nearly pure stands with minor herbaceous and shrub associates (Campbell and Franklin 1979; Page 1979). Schneller (1979) indicates that individual lady fern prothalli usually germinate together in densely packed colonies. Young prothalli may considerably influence the germination of spores and the development of other prothalli in their vicinity through the secretion of hormonal substances.

Phenology: Page (1982) notes that most lady fern fronds emerge in a single spring flush, but Schneller (1979) observes that the sporophyte continues to develop new leaves throughout the growing season. In Great Britain, lady fern fronds reach maturity by about late July (Page 1982). Although, spores generally become mature towards the end of the growing season, variation in the development of individual fronds ensures that spore dispersal is spread over a lengthy period. In Scotland, spore production of most species begins in June and carries on until late September (Page 1979). The onset of fall senescence of lady fern fronds appears to be closely tied to the date of the first frost (Page 1982). In the western Oregon Cascades, this occurred in early October, and senescence proceeded at a fairly steady rate with only 25% of the fronds remaining by early November (Campbell and Franklin 1979).

REPRODUCTION

Spore Production and Dispersal: Most medium-sized forest ferns begin to produce spores at between 1 and 5 years of age and production takes place regularly from year to year with little weather-induced fluctuation. Habitat, through its influence on plant vigour, is probably the major controlling factor of spore production (Page 1979). Lady fern reproduces more copiously than most other ferns (Frye 1934). A single fertile frond is estimated to contain 15–20 million spores (Page 1979; Schneller 1979). The tiny spores are ejected into the air by a natural dehiscence mechanism and are carried away by gravity, wind, water, or animal vectors. Fern spores are capable of travelling great distances across oceans and continents, but dispersal of spores is often limited by the absence of air currents in undisturbed forest habitats. Airborne spores are often brought to earth during rainstorms (Page 1979).

Spore Viability and Germination: Fern spores in a dry, resting state are quite resistant to physical extremes. They can withstand intense radiation and very low temperatures, but are reportedly very sensitive to temperatures above 55°C (Kato 1963; Miller 1968). Lady fern spores remain viable for about 3 years in storage. Spores that overwinter on the dead frond are often still viable in spring, and spores in soil remain

viable for at least 1 year (Schneller 1979). However, their viability and speed of germination deteriorates with age (Page 1979). Spore germination rates ranged from 50 to 95% under experimental conditions (Schneller 1979).

Spores will generally not germinate until after a period of water imbibition (Page 1979). Lady fern spores most often germinate in unexposed places on bare soil or occasionally on decaying wood (Schneller 1979). They normally require light for germination (Weinberg and Voeller 1969), but hormones secreted by nearby prothalli can stimulate germination in the dark (Schneller 1979). The great majority of spores disappear into the forest floor without germinating.

Vegetative Reproduction: Vegetative reproduction in lady fern is achieved through division of the rhizome. The rhizome occasionally branches, and in old plants may develop into large clumps with numerous closely packed crowns (Page 1982). However, unlike the bracken fern, lady fern does not form an extensive, laterally spreading rhizome. Although the species often forms large, uniform stands, these are populations of individual sporophytes rather than clonal colonies.

PREDATION AND PESTS

Ferns are extraordinarily free of the damaging effects of animals, insects, and microbial pathogens (Page 1979). Reasons for this resistance may include low levels of suitable metabolites or the presence of tough tissues and/or special repellant chemicals. The annual shedding of fronds may also serve as a protective mechanism against disease and insect infestations. In coastal B.C., fiddleheads and mature fronds of lady fern are readily eaten by black and grizzly bear, and by deer (Pojar *et al.*;[23] T. Hamilton, pers. comm., Jan. 1985).

EFFECTS ON CROP TREES

Competition: Throughout most of its range, lady fern is not considered to be a major threat to the establishment of coniferous tree seedlings. However, because it is one of the largest herbaceous plants in B.C. and because it often occurs in dense, pure stands, it can be a serious local competitor wherever it is abundant and vigorous. It is extremely abundant and a serious silvicultural problem in the SBSf subzone east of Prince George (C. Delong, pers. comm., Nov. 1984), and on hygric and wetter ecosystem associations in heavy snowfall areas of the ICH and ESSF in southeastern B.C. (D. Lloyd, pers. comm., Nov. 1984).

In the CWH zone lady fern is a dominant herbaceous plant on floodplain sites and skunk cabbage swamps and can be an important secondary competitor following logging. However, Brand did not consider it a significant competitor on five productive clearcut sites he studied in the CWH near Vancouver.[24] Vigorous growth of lady fern can shade out and crowd out young seedlings, but the smothering and mechanical damage caused by the shedding of fronds is considered to be of equal—if not greater—importance (D. Lloyd, pers. comm., Nov. 1984).

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Lady fern does not appear to increase significantly following logging, and should probably be considered a serious potential competitor only if it is well established on a site prior to canopy removal. It will probably diminish in cover on those sites where previously moist soils become prone to drying out following logging. Eis (1981) did not report any increase in lady fern cover on four different site types 6 years following logging in the SBS zone north of Prince George. Lady fern was common in moist shaded situations on the Devil's club and Alluvium site types, but had little actual cover on either. Brand noted that lady fern occurred only in undisturbed patches on recent clearcuts in the CWH near Vancouver, but reappeared 3–4 years after logging, once other vegetation was well established.[25]

Fire: Lady fern showed a slight decrease in cover following logging and prescribed burning in successional studies in Washington and northern Idaho (Mueggler 1965; Dyrness 1973).

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[23] J. Pojar, T. Lewis, H. Roemer, and D.J. Wilford. 1981. Relationships between introduced deer and the plant life of the Queen Charlotte Islands, British Columbia. B.C. Min. For., Smithers, B.C. Unpublished report.

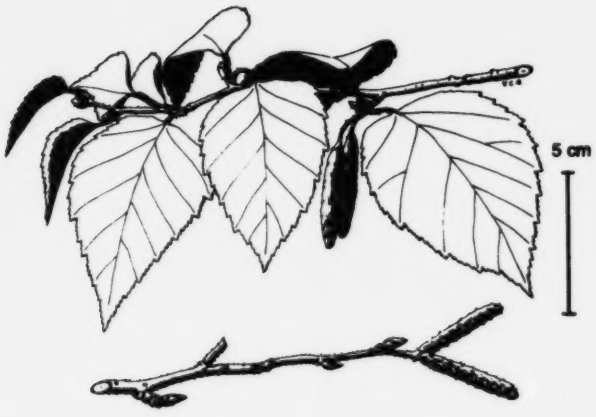
[24] Brand, 1984.

[25] Ibid.

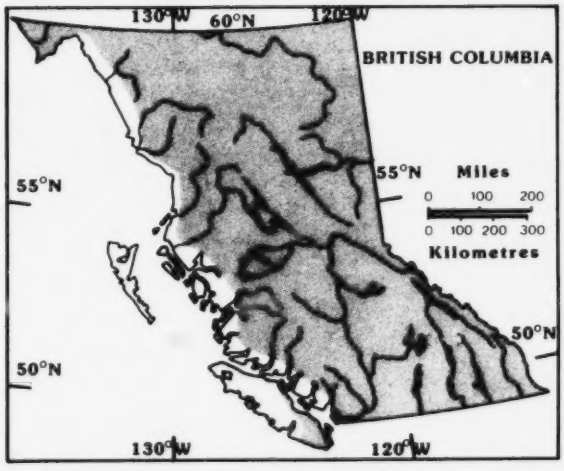
Cutting: No information.

Herbicides: Glyphosate applied either by backpack spray or aerially at 2.25 kg/ha reduced lady fern cover by 80–95% for at least one growing season in a study carried out near Prince George (Expert Committee on Weeds 1984).

Soil Disturbance: No information.



Betula papyrifera (paper birch).



Distribution of *B. papyrifera* in British Columbia.

Betula papyrifera Marsh.

Paper birch
(white birch, canoe birch)

DESCRIPTION

Paper birch is a deciduous tree to 30 m tall, often multistemmed. The characteristic bark is white or cream-coloured, with conspicuous dark, horizontally elongated lenticels, and readily peels in sheets. Twigs are slender, pubescent, or glandular with fine, pointed buds. Leaves are variable in shape, ovate with single or double serrations. Separate male and female catkins are pendulous when mature. Female catkins release large quantities of small, wide-winged fruit (Hosie 1973; Brayshaw 1978).

Variation: Paper birch is probably the most variable tree species in Canada. Many geographic varieties have been described, some of which are quite difficult to recognize. It also hybridizes extensively with other birch species. Recognized varieties in British Columbia include the common var. *papyrifera*, which occurs across Canada and is found in the Interior of B.C.; var. *commutata*, the coastal form found in the Fraser Valley, on southern Vancouver Island and scattered along the Coast; and var. *subcordata* which results from the crossing of paper birch and water birch *(B. occidentalis)* (Dugle 1966; Taylor and MacBryde 1977; Brayshaw 1978). This discussion deals primarily with var. *papyrifera*.

DISTRIBUTION AND ABUNDANCE

Paper birch is one of the most widespread tree species in northern North America. It is found throughout B.C. but is sporadic on the outer Coast. It is confined to southeastern Vancouver Island and is absent from the Queen Charlotte Islands (Calder and Taylor 1968; Brayshaw 1978). Paper birch is common in most low- to medium-elevation biogeoclimatic zones in the Interior. It is sporadic in the CWH and CDF zones, and absent from the CCPH, ESSF, MH, SWB, and AT. It is most abundant in warm, moist Interior valleys.

Altitudinal Range: Paper birch is found over a wide range of elevations, but is primarily a species of low to moderate elevations. It is absent from subalpine forests.

HABITAT

Climatic Range: Paper birch is adapted to a wide range of climates from humid to boreal and can tolerate wide variations in the patterns and amount of precipitation. It is tolerant of cold climates and grows to the northern limit of tree growth (Fowells (compiler) 1965). In B.C., paper birch is especially abundant in areas of transitional climate, lying in the Coast/Interior ecotone or between the dry and wet belts of the Interior. It apparently cannot compete well in the perhumid climate of the outer B.C. coast and is absent from most areas receiving extremely heavy snowloads.

Site and Soil Conditions: Paper birch is found on a wide variety of parent materials and on soil textures ranging from gravelly sands, to loams, to organic soils. It is most abundant on rolling upland terrain or on alluvial sites, but is also found on open slopes, rock slides, bogs and swamp margins. Best growth occurs on well-drained sandy or silty soils; or on soils derived from limestone (Fowells (compiler) 1965; Hosie 1973; Brayshaw 1978; Krajina *et al.* 1982; Marchant and Sherlock 1984).

Nutrient Relations: Paper birch grows on soils ranging from acidic to highly calcareous (Fowells (compiler) 1965). It tolerates acid soils with a pH as low as 4.4 (Balsillie *et al.* 1978, cited by Marchant and Sherlock 1984). Krajina *et al.* (1982) describe the nutritional requirements of birch as moderate to fairly high, especially for calcium and magnesium. They indicate that it prefers nitrates to ammonium as a nitrogen source.

Water Relations: Paper birch has a high tolerance to flooding and poorly drained soils (Krajina *et al.* 1982; Marchant and Sherlock 1984), but it is not commonly found in very wet situations (Fowells (compiler) 1965). In B.C. it is most often found on sites ranging from subxeric or submesic to subhygric (Angove and Bancroft 1983; R. Coupé, pers. comm., Nov. 1985). Growth is best where the soil is moist but well drained.

Light Relations: The shade tolerance of paper birch is low (Hosie 1973; Krajina *et al.* 1982). Paper birch is most abundant as an overstory tree in seral forest, and does not occur as an understory species, becoming restricted to openings as the forest matures (Hosie 1973). Although germination is best in the shade, subsequent seedling growth is favoured by full sunlight. Paper birch seedlings grown in full sunlight had larger roots and a higher root-shoot ratio than seedlings grown in partial shade (Marquis 1966).

Temperature Relations: Paper birch is very frost resistant and can easily tolerate frozen ground (Krajina *et al.* 1982). Seasonal growth often begins while (minimum) temperatures are below freezing (Fowells (compiler) 1965). In Alaska it grows in soils with the frost layer near the soil surface throughout much of the growing season (Foote 1983). Equally, it seems able to tolerate some of the hottest summer temperatures to be found in B.C. as long as sufficient moisture is available.

GROWTH AND DEVELOPMENT

Paper birch does not exhibit the rapid early growth that characterizes other hardwood species such as black cottonwood and red alder. Paper birch seedlings average 10 cm in height after the first growing season (Fowells (compiler) 1965) and can reach a maximum of 40 cm on favourable sites in full sunlight (Marquis 1966). Grant and Thompson (1975) report that 3-year-old birch in B.C. average 32 cm in height, whereas, in Alaska, a maximum height of 25 cm in 3 years was reported (Zasada *et al.* 1983). Fowells (compiler, 1965) reports that 4-year-old birch average 1 m in height. Growth of sprouts is considerably more rapid than that of seedlings. Sprouts can grow up to 60 cm in the 1st year and are twice as tall as seedlings after 4 years.

Birch reaches maximum heights of 30–40 m at maturity and diameters as large as 1 m at the base. The tree has a narrow, oval crown when it grows in the forest, but in openings, the crown spreads out from near the base. Many trees develop a broad, multistemmed crown, particularly following disturbance. Paper birch is considered a short-lived species. Trees mature and cease height growth at 60–70 years and few live longer than 140 years. The tree has a deep, penetrating root system (Fowells (compiler) 1965; Hosie 1973; Marchant and Sherlock 1984).

Phenology: Paper birch begins flowering in mid-April in southern areas and flowers during May and June in Alaska. Flowering takes place before the leaves expand. Height growth begins early in the growing season while temperatures are still quite cool, while diameter growth starts after maximum temperatures reach 21°C. The seed normally ripens during August and September with dispersal beginning immediately after ripening and continuing through to the following January. However, seed dispersal as early as July has been reported in Alaska. Opening of the mature female catkins is stimulated by low humidity and frost (Fowells (compiler) 1965; Zasada 1971; Viereck and Little 1972; Marchant and Sherlock 1984).

REPRODUCTION

Seed Production and Dispersal: Seed production begins at about age 15. Paper birch trees produce good seed crops every 2 years. Seeds are winged nutlets that are dispersed by wind and water; they are often blown for long distances on crusted snow. Although the seed is light and travels easily, the majority of the seed falls within 100 m of the parent tree (Fowells (compiler) 1965; USDA 1974; Archibold 1980).

Seed Viability and Germination: The quality of paper birch seed is highly variable. In heavy seed years a high percentage of the seed is good (USDA 1974). Seed quality averaged 17% in four undisturbed Alaska stands with a low of 1% and a high of 42% (Zasada 1971). Seed remains viable for up to 2 years if the moisture content is low, but degenerates rapidly in moist conditions (USDA 1974). Exposure to a period of low temperatures significantly improves germination percentages (Nichols 1934). Germination normally takes place the spring following seed dispersal. Germination is best in the shade, on areas where the mineral soil and organic layers are mixed, where ample moisture is available, and where surface temperatures are moderate (Marquis 1966). Humus is satisfactory for germination but not as favourable as mineral soil or mixed materials. Leaf litter is a poor medium for germination. Best initial growth was observed on organic seed beds (Marquis *et al.* 1964). An Alaska study found that germination was equal on both north and south aspects with virtually all germination taking place in mid to late June (Viereck and Dyrness 1979).

Vegetative Reproduction: Paper birch will sprout from the root collar and from the stump. Prolific sprouting will occur when trees are young, but sprouting vigour decreases with age. Sprouting may occur at the base of standing, live trees that have been subjected to increased exposure by disturbance (Fowells (compiler) 1965). Paper birch can be propagated by cuttings, but fragments are unlikely to root in nature. Vegetative reproduction is important for the persistence of individual trees following disturbance, but is less important than regeneration from seed as a means of reproduction of the species (Lutz 1955).

PREDATION AND PESTS

Paper birch is browsed by deer and moose, and is an important food for beaver. Many small mammals nibble at the stem or bark, and can girdle or damage the tree, especially when it is young (Stoeckeler 1955). Birds feed on the buds, catkins, and seed.

The principal disease and insect pests of paper birch are described by Fowells (compiler, 1965).

EFFECTS ON CROP TREES

Competition: Paper birch is not as serious a competitor as aspen in the Interior,[26] and is too scattered to be a significant competitor on the Coast. However, it can be a serious local competitor where there are concentrations of mature birch and where harvesting and silvicultural practices favour seeding-in. Early growth is more rapid than that of white spruce (Arlidge 1967), and where paper birch seeds in densely, or has sprouted from stumps, it can compete severely with interior conifers. Gregory (1966) found that only an occasional white spruce can become naturally established beneath birch stands in Alaska. Crushing and smothering beneath birch litter causes a high rate of mortality among spruce germinants.

Beneficial Effects: No beneficial effects of paper birch on conifer growth are described in the literature. The deep rooting habit of the species, its relatively high demand for soil nutrients, and the rapid turnover of deciduous foliage suggest that soil organic matter content and associated levels of nutrients may be higher under birch than under a purely coniferous stand.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Seeding-in of paper birch will normally be abundant where seed trees are left standing and logging disturbance has created a suitable seedbed. However, most seed is confined to within 100 m of standing trees (Archibold 1980). The sprouting vigour of mature trees cut during logging is variable; mortality of sprouts is usually high (Fowells (compiler) 1965).

Fire: Paper birch bark is thin and highly flammable, making this tree highly susceptible to fires of even moderate intensity (Lutz 1955; Fowells (compiler) 1965). Sprouting is common on trees damaged or killed by fire (Hosie 1973), but sprouts are less frequent on middle-aged and old trees than in young stands (Lutz 1955). Paper birch thrives in an environment with a regular fire history and regeneration is frequently more common on burned areas than on unburned areas (Behrend and Patrick 1969). In the eastern U.S., stocking was 2 or 3 times greater on burned areas than on either summer or winter logged areas receiving no site preparation (Bjorkbom 1967).

Cutting: Prolific sprouting from either the root collar or the stump usually occurs when young, vigorous trees are cut in the spring to stump heights of 15-30 cm (Fowells (compiler) 1965). Approximately 97% of cull trees that were either notch girdled or double-frill girdled were dead or seriously damaged 4 years after treatment (Crombie 1965). Twenty-one percent of the stems sprouted following treatment, single-frill girdling was ineffective, and addition of 2,4,5-T to the girdled area reduced suckering but was not considered necessary.

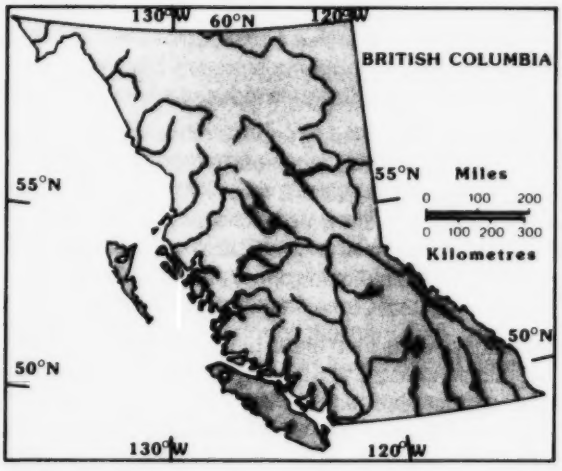
Herbicides: Glyphosate was highly effective in killing paper birch when applied as a foliar spray at rates of 2.24 kg a.i./ha and greater in Ontario (Sutton 1978). Glyphosate (20% solution: 2 ml per 7.5 cm dbh), hexazinone (pure: 2 ml per 7.5 cm dbh), and triclopyr (pure: 2 ml per 7.5 cm dbh), applied by hypohatchet, killed or seriously injured all paper birch trees in a New Brunswick study (Wile 1981). Good control of paper birch was achieved with a foliar spray of 2,4-D ester at 3 kg a.i./ha in the Vancouver Forest Region (M. Scott, pers. comm., Nov. 1984). Hexazinone applied by liquid spray, spot gun and in granular form has produced variable rates of defoliation and mortality (Expert Committee on Weeds 1984).

Soil Disturbance: Paper birch readily seeds in to areas of mineral soil exposed during logging or mechanical site preparation.[27] In Maine, stocking was 2 to 3 times greater on mechanically site-prepared areas than on winter or summer logged areas that received no treatment (Bjorkbom 1967). Soil disturbance that mixes mineral and organic soil layers is favourable to germination of paper birch seed (Marquis *et al.* 1964).

[26] J. Revel. 1983. The impact of some hardwoods on silviculture in the Prince George Forest Region. B.C. Min. For., Prince George, B.C. Unpublished discussion paper.

[27] Perry, 1983.

Calamagrostis canadensis (bluejoint).



Distribution of *C. canadensis* in British Columbia.

***Calamagrostis canadensis* (Michx.) Beauv.** **Bluejoint**
(C. scribneri) (marsh reed grass, Scribner's reed grass)

DESCRIPTION

Bluejoint is a perennial, tussock-forming grass with stems 60-120 cm tall and creeping rhizomes. The leaf blades are elongate, slightly drooping and flat, 10–30 cm long and 4–8 mm wide. The inflorescence, or seedhead, is a drooping panicle that varies from narrow and rather dense to loose and open, and often has a purplish tinge (Hubbard 1969; Hitchcock and Cronquist 1973).

Variation: Bluejoint is a widely distributed and exceedingly variable species (Hitchcock 1971) with various subspecies and varieties recognized by different authors. Taylor and MacBryde (1977) have broken out a separate species, *C. scribneri* (Scribner's reed grass), to describe varieties found in the central and northern Interior of British Columbia that have traditionally been considered part of *C. canadensis*. *Calamagrostis scribneri* has been included as part of *C. canadensis* in this discussion, and the name "bluejoint" used to refer to the entire complex.

DISTRIBUTION AND ABUNDANCE

Bluejoint is found throughout B.C. in every biogeoclimatic zone. It is more abundant and occurs over a wider range of sites in the Interior than on the Coast. It is most common in the northern half of the province and at higher elevations in southern B.C. (Hubbard 1969; McLean 1979).

Altitudinal Range: Bluejoint is found from sea level to the alpine tundra zone.

HABITAT

Climatic Relations: Bluejoint is able to tolerate a very wide range of climates, as shown by its extremely broad geographic distribution within western North America. It seems to be particularly well adapted to a harsh northern climate since it reaches its greatest abundance and best development in Alaska and northern Canada (Mitchell 1974; Watson *et al.* 1980). It can tolerate very exposed conditions (Mitchell 1978, cited by Watson *et al.* 1980) and is extremely winter hardy (Alaska Rural Development Council 1977, cited by Watson *et al.* 1980).

Site and Soil Conditions: Throughout much of southern B.C., bluejoint is primarily a wetland species, occurring in swamps, marshes, wet meadows, and floodplains. In the SBS and particularly in the BWBS zone, it is also a common grass on upland sites (Hubbard 1969; McLean 1979; Pojar *et al.* 1982). Bluejoint is found on both mineral and organic soils. In the subarctic, it occurs most often on peaty soils (Watson *et al.* 1980), while in Manitoba it is found predominantly on fine-textured soils with good water-holding capacity and on sandy soils with high water tables (Mueller-Dombois and Sims 1966). In southeastern B.C., it occurs mainly on gleyed or organic soils (Comeau *et al.* 1982); in northern B.C. and Alberta, it is found in openings on moist forest sites and along streambanks, and it commonly invades clearcuts and a wide variety of disturbed soils (Blackmore and Corns 1979; Watson *et al.* 1980; Eis 1981).

Nutrient Relations: Bluejoint is thought to have moderate nutritional requirements (Alaska Rural Development Council 1977, cited by Watson *et al.* 1980). In Alaska, it grows in moderately to strongly acidic soils ranging from pH 5.5 to 3.5 (Mitchell 1974). Comeau *et al.* (1982) report that it is found on sites ranging from very poor (oligotrophic) to very rich (eutrophic) in nutrient status. Additions of nitrogen, phosphorus, and potassium can greatly increase growth rates (Mitchell and Evans 1966).

Water Relations: Bluejoint is characteristically a species of wet to moist sites, but it can survive a wide range of moisture regimes (Watson *et al.* 1980). Mueller-Dombois and Sims (1966) grew *C. canadensis* under a range of moisture conditions in a sloping tank and concluded that its dominance on wet to moist sites in Manitoba is attributable to its tolerance of, rather than preference for, such localities. *Calamagrostis canadensis* seedlings had the lowest drought tolerance of the three grass species tested by the previous authors, but once the root system is well established drought tolerance is apparently good. It is also very tolerant of flooding and saturated soil conditions (Alaska Rural Development Council 1977, cited by Watson *et al.* 1980).

Light Relations: Bluejoint is most abundant and reaches its best development on open sites, but it will also tolerate partial shade (Watson *et al.* 1980). It appears to be adapted to grow very rapidly during the long daylight regime of early to midsummer in northern latitudes (Mitchell 1974)

Temperature Relations: The root system of bluejoint is tolerant of low soil temperatures (Younkin 1974, cited by Watson *et al.* 1980)

GROWTH AND DEVELOPMENT

Bluejoint is a long-lived, mat-forming perennial grass that often reaches 60–120 cm in height (Hubbard 1969). Watson *et al.* (1980) report that it is slow to establish itself, but in growth experiments by Sims and Mueller-Dombois (1968), *C. canadensis* had produced a continuous, dense sod of roots after 1 year. The sod was 1–2 cm thick on a poor sandy soil and 4–8 cm thick on a loamy sand. The fine roots were intermingled with numerous rhizomes (Mueller-Dombois and Sims 1966). On logging sites, bluejoint can form continuous mats as early as the 3rd or 4th year following logging (Frisque *et al.* 1978, cited by Eis 1981). Once established, bluejoint can grow quickly. Mitchell (1974) reports that luxuriant stands in southcentral Alaska can grow to heights of over 150 cm during a 6-week growing period. In trials in the northern boreal forest reported in Watson *et al.* (1980), biomass and cover of bluejoint equaled or exceeded those of commercial grass species by the end of the first growing season. The above-ground parts of bluejoint die back at the end of each growing season, producing a thick organic mulch. During the growing season, dead leaves comprise approximately 50% of the total above-ground biomass in a stand of bluejoint (Sylvester and Wein 1981).

Phenology: In southcentral Alaska, bluejoint completes its height growth by mid-July (Mitchell 1974) and is fully headed by mid-August (Mitchell and Evans 1966).

REPRODUCTION

Seed Production and Dispersal: Like other grasses, bluejoint is adapted for wind pollination and seed dispersal (Hitchcock 1971). The drooping panicle moves readily in the wind, and seeds are easily windborne. Bluejoint rapidly seeds-in to disturbed sites (Watson *et al.* 1980; Rowe 1983). Seed is produced annually, provided that environmental conditions are favourable, but seed yields are reportedly low (Younkin 1974, cited by Watson *et al.* 1980).

Seed Viability and Germination: Younkin (1974, cited by Watson *et al.* 1980) reported a germination rate of 90% in seed from Inuvik, N.W.T. Germination occurred without cold stratification. Mueller-Dombois and Sims (1966) also observed very high rates of germination after 3 days on both sandy and loamy sand soils when the soils were wetted to field capacity. Germination apparently will not occur under droughty conditions (Wein and McLean 1973).

Vegetative Reproduction: Bluejoint is a rhizomatous grass species (McLean 1979), and once it has seeded-in to an area, further spread is primarily by rhizomes (Wein and Bliss 1973; Watson *et al.* 1980).

PREDATION AND PESTS

No references to insect or microbial pests were found in the literature. Bluejoint is moderately palatable but not highly favoured by domestic livestock (McLean 1979).

EFFECTS ON CROP TREES

Competition: Bluejoint is a significant competitor with crop trees in the BWBS, SBS, and ESSF biogeoclimatic zones and provides relatively minor localized competition on wet sites in other zones. It is of particular importance in the boreal forest of the Prince George Forest Region where it is extremely abundant in clearcut areas. Root competition with young seedlings is considered to be the dominant mode of competition. Bluejoint roots in the same zone as young tree seedlings and produces a very dense, continuous sod (Sims and Muller-Dombois 1968). Sims and Mueller-Dombois showed that the effect on tree growth was most severe not on the driest sites and sandiest soils, but on relatively moist, loamy soils where *Calamagrostis* was most vigorous. On the driest sites, the young seedlings were able to get their roots below the shallow, poorly developed grass sod.

Bluejoint can also shade out young seedlings and the heavy litter causes snow press and smothering (Arlidge 1967; Blackmore and Corns 1979; Eis 1981). Eis also noted that thick mats of grass prevent natural regeneration by conifers. Conifer seeds falling into the grass are suspended above the soil and the

germinants dessicate as the grass dries out in spring. Bluejoint may also indirectly reduce seedling growth in northern latitudes by preventing soils from warming up during the growing season. Mitchell (1974) notes that thick layer of litter and mulch that develops under a bluejoint cover has a significant insulating effect on the soil.

Beneficial Effects: The high ground cover and dense root mat of bluejoint provides good control against surface soil erosion (Watson *et al.* 1980). Blackmore and Corns (1979) speculate that a light growth of bluejoint on a scalped area of soil may be beneficial in reducing frost-heaving of seedling conifers. No other beneficial effects of the species on tree growth are documented in the literature, but it undoubtedly increases soil organic matter content, particularly on heavily disturbed sites. A cover of bluejoint can also limit invasion of larger brush species that may have a longer-lasting and more serious impact on crop tree growth.

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Bluejoint increased significantly on three moist site types north of Prince George following clearcut logging (Eis 1981). On the Alluvium site type it invaded all areas not covered by shrubs, and thick continuous mats had formed by the 3rd or 4th year following logging.

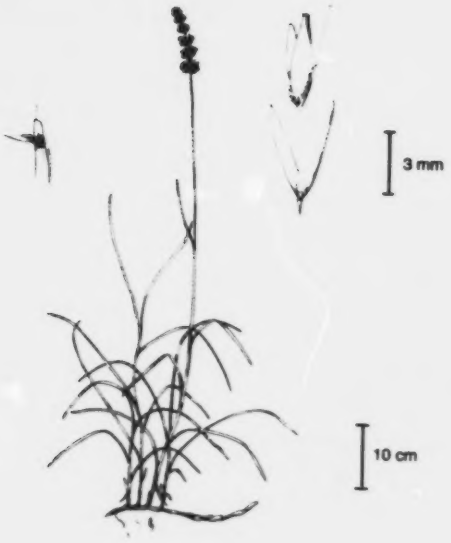
Fire: Bluejoint is a major invader following fire in the arctic tundra (Wein and Bliss 1973). Small plants present prior to burning lacked vigour and did not produce seeds, but their rhizomes survived the fire and cover increased four-fold under the new growing conditions. In northern Minnesota (Ahlgren 1960), bluejoint also occurred widely the 1st year after burning and did not appear to be affected by fire severity. Reproduction was primarily by rhizomes but some seedlings were established by windborne seed. Sylvester and Wein (1981) point out that fire spreads rapidly through stands of bluejoint because of the large volumes of fine, dry litter present. Live plant material is very resistant to burning but does not slow down the rate of fire spread.

Cutting and Grazing: Bluejoint is intolerant of heavy cropping (Mitchell and Evans 1966). Yields decreased by up to 20% when the grass was cut 2–4 times during the growing season and by 70% when cut 7 times (Corns and Schraa 1962).

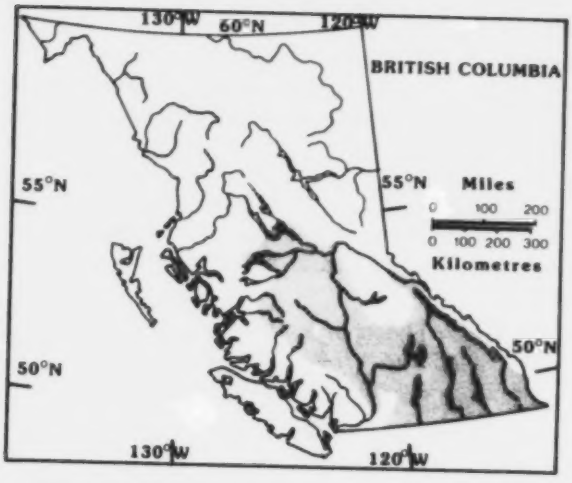
Herbicides: Glyphosate applied in June, July, or August as a foliar spray at rates of 2.2–4.5 kg/ha has provided good to excellent control of bluejoint (Blackmore and Corns 1979; Expert Committee on Weeds 1984). Blackmore and Corns found that glyphosate applied in August (at 2.2 kg/ha) gave better control than the same rate applied in June. Hexazinone applied as a liquid spray at rates of 1.1–4.3 kg/ha has also provided excellent control of bluejoint; however, with increasing organic matter depths, results become less consistent (Expert Committee on Weeds 1984).

Soil Disturbance: Bluejoint aggressively invades disturbed sites. Invasion is by seed or through rhizomes from adjacent areas (Watson *et al.* 1980). North of Prince George, bluejoint invaded most heavily on moist to wet compacted soils on roads, landings, and skid trails on the Alluvium site type (Eis 1981). Arlidge (1967) found that within 2-3 years following scarification, bluejoint was a serious competitor on mounded microsites within wet depressional areas. In the Peace River region of B.C., L.J. Herring (pers. comm., March 1985) has found that bluejoint spreads onto disturbed ground first by rhizome extension, and thereafter by seed. Heavy cultivation substantially controls established plants, but areas of newly exposed soil are rapidly reinvaded by adjacent, undisturbed plants.

Fertilization: Fertilization with nitrogen, phosphorus, and potassium caused major increases in production of bluejoint in southcentral Alaska (Mitchell 1974). In the Northwest Territories, fertilization markedly stimulated flowering rates and increased vegetative growth (Hutchinson and Hellebust 1978, cited by Watson *et al.* 1980).



Calamagrostis rubescens (pinegrass).



Distribution of *C. rubescens* in British Columbia.

Calamagrostis rubescens Buck. — Pinegrass

DESCRIPTION

Pinegrass is a slender, tufted grass, with creeping rhizomes. It is 60–100 cm tall when flowering, but only 30–50 cm in the more common vegetative state. The stems have a reddish tinge at the base and a ring of hairs where the leaf meets the stem. The leaf blades are erect, 2–4 cm wide, flat or somewhat rolled, and are rough to touch. The inflorescence (seedhead) is a congested, narrow panicle 7–15 cm long, pale or with a purplish tinge (Hitchcock 1971; McLean 1979; Angove and Bancroft 1983).

Variation: This species is found only in western North America, from southern British Columbia to California. There are no varieties or subspecies described in B.C. (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Pinegrass is found throughout the central and southern Interior of B.C. It is absent from the west side of the Coast Mountains and extends only as far north as Francois Lake and Fort St. James in the Interior. Pinegrass is the most abundant grass in forested areas of the southern Interior. It is the dominant understory species in the IDF zone and is common in most subzones of the SBS and MS zones. It also occurs in drier subzones of the ICH and ESSF, at low elevations and in moist areas of the PPBG zone (McLean 1979; Angove and Bancroft 1983).

Altitudinal Range: Pinegrass ranges from the valley bottoms of the Interior to subalpine elevations. It is absent from the lower elevations of the PPBG zone. It is found between 600 and 1850 m in the Similkameen Valley (McLean 1970), while in the moister climate of northern Idaho it is most abundant in the 850–1000 m elevation band (Mueggler 1965).

HABITAT

Climatic Relations: The geographic distribution of pinegrass in B.C. suggests that it favours a continental climate with warm, dry summers, and can tolerate moderately cold—but not extreme—winter temperatures. It is not present in areas of high precipitation, and it is absent from the hottest, semi-desert areas of the southern Interior. Tiedemann and Klock (1974) observed that it was most abundant on south aspects in Washington, while Mueggler (1965) found no preference for aspect in northern Idaho.

Site and Soil Conditions: Pinegrass is found on a wide variety of well-drained sites within its geographic range. Ecosystems in which pinegrass is a characteristic dominant understory species have a wide variety of parent materials, slopes and soil characteristics, but soils are most often well drained, loamy to coarse textured Luvisols and Brunisols (see e.g., Freyman and van Ryswyk 1969; McLean 1970; Mitchell and Green 1981; Coupé and Yee (editors)[28]). In the ESSF zone of the Similkameen Valley, *C. rubescens* is virtually absent on shallow rocky soils and is sparse on Podzolic soils (McLean 1970). Mueggler (1965) noted that pinegrass was frequently found on steeply sloping sites in the cedar-hemlock zone of northern Idaho.

Nutrient Relations: In the SBS zone, pinegrass occurs on sites ranging from very low (oligotrophic) to moderately high (permesotrophic) in nutrients (Pojar *et al.* 1982). In southern B.C., it is a characteristic species of ecosystem associations with a wide range of nutrient regimes from very poor to very rich (see e.g., Mitchell and Green 1981; Utzig *et al.*[29]). McLean and Tisdale (1960) and McLean *et al.* (1969) have conducted detailed studies on the chemical composition of pinegrass. It has low levels of calcium and phosphorus compared with other forest understory and grassland species. The level of phosphorus declines over the growing season while the level of calcium increases. Soils supporting a heavy growth of pinegrass are frequently low in nitrogen, and increasing the levels of nitrogen, nitrogen and sulphur, or phosphorus stimulates growth of pinegrass (Freyman and van Ryswyk 1969).

Water Relations: There are no studies of the water relations of pinegrass. Throughout B.C., it tends to be associated with soils that experience at least moderate moisture deficits during the growing season. The ecological moisture regime of sites with abundant pinegrass varies considerably depending on climate. In the IDF zone where it is most abundant, pinegrass occupies extremely xeric to hygric sites (Angove and Bancroft 1983). The ability of pinegrass to regrow following grazing in midsummer depends on the availability of water in surface soil horizons (Freyman and van Ryswyk 1969).

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[28] Coupé and Yee (editors), 1982.

[29] Utzig *et al.*, 1983.

Light Relations: Pinegrass is variously described as moderately shade-tolerant (Crane *et al.* 1983) to very shade-intolerant (B. Mitchell, pers. comm., Nov. 1984). Throughout its range in B.C., it occurs in the understory of fairly open forests of pine and Douglas-fir, but under these conditions it rarely flowers. Flowers and seeds are produced in open situations such as burns and clearcut areas (McLean 1979; Crane *et al.* 1983). The shade tolerance of pinegrass appears to vary with elevation and accompanying moisture and temperature conditions. McLean (1970) reports that between 600 and 900 m in the Similkameen Valley, pinegrass is present under Douglas-fir but declines when stands are opened up. In the ESSF zone between 1350 and 1850 m, pinegrass cover varies greatly with the amount of shade and is most abundant in stand openings on south aspects.

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

In the understory of forest stands, pinegrass forms a loose, open turf connected by a system of creeping rootstocks or rhizomes (McLean 1979). Fine fibrous roots are produced at each node of the rhizome (Hitchcock 1971). The rhizome and root system develops into a continuous dense mat, but it tends to be shallow in depth and may establish itself more slowly than the root system of a non-rhizomatous grass species such as orchardgrass (Clark and McLean 1975).

Phenology: McLean and Tisdale (1960) collected flowers of pinegrass on 16 July, early seed on 5 August, and late seed on 2 September near Kamloops. Vegetative growth of pinegrass is available for grazing in the Kamloops and Cariboo Forest Regions between early May and late October (McLean *et al.* 1969).

REPRODUCTION:

Seed Production and Dispersal: Pinegrass does not normally produce seed except in forest openings (McLean 1979; Crane *et al.* 1983). Seeds are produced in erect, spike-like panicles, and dispersal is probably primarily by wind as with other grass species (Hitchcock 1971).

Seed Viability and Germination: In germination studies carried out by McLean (1967), maximum germination of pinegrass was 38%. Neither stratification nor scarification of the seed are necessary to induce germination. The lack of a chilling requirement suggests that pinegrass is adapted to germinate whenever an adequate supply of moisture is available, and that fall germination is a possibility (v. Grime 1979).

Vegetative Reproduction: The primary method by which pinegrass establishes and regenerates is through the lateral extension of creeping rhizomes (McLean 1979; Crane *et al.* 1983).

PREDATION AND PESTS

Pinegrass is a principal species for summer grazing of cattle in south and central B.C. (McLean *et al.* 1969). Grazing preference by cattle is moderate in spring but declines as the grass matures. Pinegrass grown in full sunlight in forest openings and burns is eaten more readily by cattle than that grown in the shade of trees (McLean and Tisdale 1960).

EFFECTS ON CROP TREES

Competition: The abundance and dominance of pinegrass in the south and central Interior of B.C. makes it of major importance as a competitor with crop trees, particularly in the IDF biogeoclimatic zone. It is generally agreed that grass competes with conifer regeneration, but the degree and causes of the competitive effect are poorly understood.[30] Competition is usually most severe on droughty sites, and root competition for moisture appears to be the dominant mode of competition. Competition for soil nutrients also occurs, and the degree of competition between pinegrass and tree seedlings may be influenced by soil fertility (Clark and McLean 1975). Shading and smothering by pinegrass are of relatively minor importance.

Tree seedlings that have not yet established a good interlocking root system compete poorly with grass for available moisture.[31] Thus, seedlings that are established prior to grass invasion have a good chance of survival, whereas those established simultaneously with, or later than, the grass will grow poorly. An experiment by Clark and McLean (1975) suggests that pinegrass provides less competition to lodgepole pine than orchardgrass (a commonly seeded, non-rhizomatous forage species) because pinegrass is slower to develop its root system.

[30] M.B. Clark. 1975. Grass-conifer compatibility: a problem analysis. B.C. Min. For., Kamloops, B.C. Unpublished report.
[31] Ibid.

Beneficial Effects: There are several possible beneficial effects of pinegrass growing in association with coniferous trees. The rhizomatous growth habit and the dense network of fine roots provide excellent control of surface soil erosion. A cover of grass incorporates valuable, nutrient-rich organic matter into surface soil layers.[32] Pinegrass may also play a role in excluding invasion of more competitive species. Clark also suggested that a cover of pinegrass may help to reduce or prevent overstocking of lodgepole pine.[33]

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: In the Similkameen Valley, pinegrass decreases in abundance following logging at lower elevations in open Douglas-fir — fescue ecosystems, but increases in abundance following canopy removal above 1200 m in the Douglas-fir — pinegrass type and in the subalpine fir forest (McLean 1970; McLean *et al.* 1971). This difference in response according to elevation may reflect the relative moisture and temperature stresses that the plant experiences following canopy removal. Thinning of dense ponderosa pine produced significant increases in pinegrass cover in eastern Washington (McConnell and Smith 1970).

Fire: Pinegrass is capable of regenerating quickly following fires of light to moderate intensity (Stickney 1981). However, because roots and rhizomes are generally found within the upper 5 cm of mineral soil, any fire that completely penetrates the duff layer can be expected to do extensive damage (McLean 1969). In the cedar-hemlock forests of northern Idaho, pinegrass was most abundant on sites that had received repeated burns over a period of 30 years (Mueggler 1965). In western Montana, pinegrass increased steadily for the 1st few years following a fire, and by the 5th year, cover was well above preburn levels (Stickney 1981).

Cutting and Grazing: Pinegrass is susceptible to heavy grazing and is often partially replaced by other species (McLean 1979). Environmental conditions, especially summer rainfall, affect the response of the species to grazing or clipping, and year to year fluctuations in growth due to environmental variability can exceed grazing treatments (Stout *et al.* 1981). Pinegrass failed to regrow when clipped in mid-July due to depletion of surface water supplies (Freyman and van Ryswyk 1969). Pinegrass was clipped throughout the summer at three levels of intensity for 4 consecutive years (Stout *et al.* 1981). Clipping to 15 cm did not significantly affect stand vigour, but the 5-cm and 10-cm clipping treatments produced a steady decline in plant yield. The largest decrease in production occurred after the 1st year of treatment, and the plants were most sensitive to herbage removal in early July.

Herbicides: Hexazinone applied as either a pre- or post-plant treatment at 2.2 kg/ha provided good to excellent control of pinegrass for two growing seasons (Dimock *et al.* 1983). Other chemicals, all unregistered in B.C., have been tested for controlling pinegrass with mixed results (see Stewart and Beebe 1974; Dimock *et al.* 1983). Stewart and Beebe found that the mulch of dead grass present after spraying may have aided survival of planted conifers by conserving soil moisture and reducing high surface soil temperatures.

Soil Disturbance: Anchor chain drag scarification has been shown to increase the cover of pinegrass significantly on some B.C. clearcut areas. Light to medium soil disturbance favours pinegrass, but heavy soil disturbance may cause a reduction in cover.[34] Patch scarification was less effective than herbicides in controlling competition by pinegrass and other seeded grasses in central Washington (Stewart and Beebe 1974).

Fertilization: Freyman and van Ryswyk (1969) tested response of pinegrass to 100–200 kg/ha of nitrogen, phosphorus, potassium, and sulphur. Nitrogen significantly increased growth and yield of pinegrass on all sites. Nitrogen combined with low levels of sulphur produced the greatest vigour, but high rates of sulphur caused some mortality of pinegrass. Phosphorus at 200 kg/ha, in combination with other nutrients, increased yields significantly. Fertilizer response was low when applied in mid-July because soil moisture was not adequate to permit absorption of nitrogen. Nutrient uptake of grass is favoured at the expense of conifers.[35] Thus, applications of fertilizer may have a detrimental effect on planted conifers because of the increased competition they face from vigorous pinegrass.

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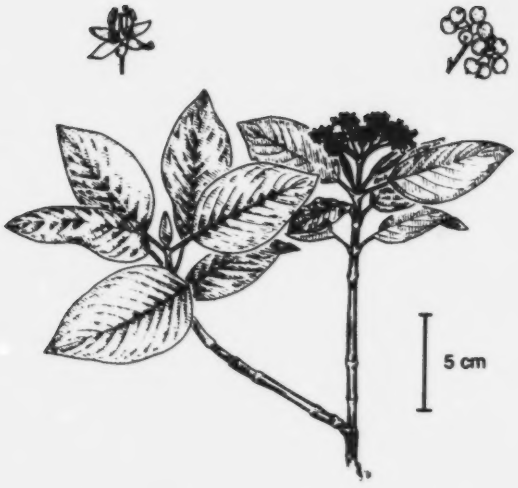
[32] W.W. Carr. Undated. The use of a grass-legume cover as a silvicultural tool (EP 834). B.C. Min. For., Research Branch. Victoria, B.C. Unpublished report.

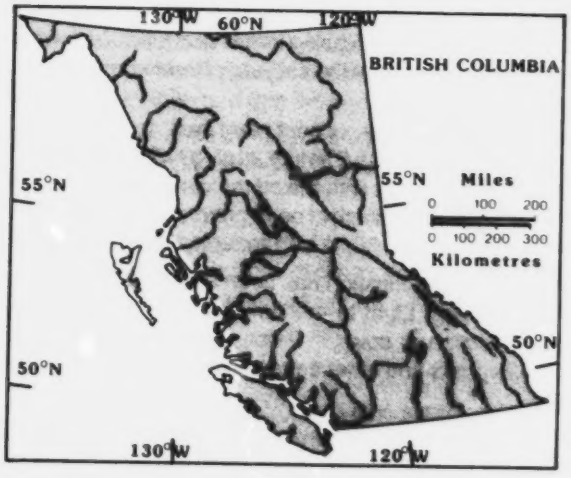
[33] Clark, 1975.

[34] Ibid.

[35] Ibid.



Cornus sericea (red-osier dogwood).



Distribution of *C. sericea* in British Columbia.

Cornus sericea L. — Red-osier dogwood
(C. stolonifera)

DESCRIPTION

Red-osier dogwood is an erect or spreading deciduous shrub, 2–5 m tall, often bearing prostrate rooting (stoloniferous) branches. The stems are oppositely branched and have smooth bark that turns bright red during the dormant season. Leaves are elliptic to ovate, untoothed with prominent, curving veins. The small white flowers are found in a flat-topped terminal cluster. Fruit is a white to bluish drupe with a single nutlet (Rickett 1944; Viereck and Little 1972; McLean 1979).

Variation: This is a confusing complex found across northern North America that is sometimes treated as a single species with several varieties, and sometimes split into several distinct species (Fosberg 1942). According to Rickett (1944), the shrub in British Columbia is taxonomically similar to the *C. sericea* or *C. stolonifera* of eastern North America, where most of the literature on this species originates. Taylor and MacBryde (1977) describe the *C. sericea* found throughout most of B.C. as a western variety, var. *occidentalis,* and state that the typical var. *sericea* occurs only in eastern and northeastern B.C. Red-osier dogwood is widely cultivated and there are many horticultural cultivars in existence. Some of these cultivars are being used as plant material for detailed physiological studies of dormancy and cold-hardiness in Oregon and Minnesota.

DISTRIBUTION AND ABUNDANCE

Red-osier dogwood is found throughout B.C., both on the Coast and in the Interior. It occurs in all biogeoclimatic zones except the AT, but is rare on the outermost Coast in the CCPH, and in the MH zone. It is most abundant in broad river valleys throughout the province.

Altitudinal Range: Red-osier dogwood is primarily a low-elevation species, although it does extend to near timberline (Lyons 1952; R. Coupé, pers. comm., Nov. 1984). In the central Rocky Mountains it extends from 1370 to 3050 m in elevation (Watson *et al.* 1980).

HABITAT

Climatic Relations: The distribution of red-osier dogwood in North America appears to be restricted by high temperatures (Smithberg 1974). In B.C., however, local site conditions rather than climatic extremes appear most limiting to the distribution of the species. The cool and extremely wet climate of the outer north Coast seems to be the least favourable to red-osier dogwood and, although it is found in northern Canada to the edge of the arctic tundra (Smithberg 1974), it does not appear to fare well in the high mountain climate of B.C.

Smithberg and Weiser (1968) studied variation among climatic races of red-osier dogwood and found that many physiological events are directly related to climatic factors such as winter temperature minima, daylength, and length of growing season.

Site and Soil Conditions: Red-osier dogwood is a characteristic species of swamps, low meadows, and riparian habitats; however it is also commonly found in open upland woods and forest margins (Smithberg 1974; Watson *et al.* 1980). In the dry Interior of B.C. it is restricted primarily to protected moist sites (McLean 1979). Red-osier dogwood is found on a wide range of soil textures and parent materials (Smithberg 1974; Alaska Rural Development Council 1977, cited by Watson *et al.* 1980), but in B.C. it is most characteristic of (and produces its best growth on) fluvial ecosystems with gleyed or regosolic soils (see e.g., Haeussler *et al.* 1984; Pojar *et al.* 1984; Coupé and Yee (editors)[36]).

Nutrient Relations: Wilde (1946, cited by Smithberg 1974) described ideal soil fertility conditions for red-osier dogwood as follows: pH 5.0–6.0; base exchange capacity 6.0 ME/100g; total nitrogen 0.7%; nitrogen 17 kg/ha ; phosphorus oxide (P_2O_5) 84 kg/ha; potassium dioxide (K_2O) 168 kg/ha; replaceable calcium 1350 kg/ha. Red-osier dogwood is tolerant of alkaline soils and found over a wide range of pH values, but plants on poor soils tend to grow more slowly and produce less fruit (Jewell and Brown 1929, cited by Smithberg 1974). In the SBS zone near Prince George, *C. sericea* has a narrow amplitude with respect to soil nutrient conditions, and occupies sites with relatively high rates of exchangeable calcium and magnesium (Wali 1969).

[36] Coupé and Yee (editors), 1982.

Water Relations: Throughout its range, red-osier dogwood is associated with moist to wet soil conditions where it is not subject to significant moisture stess (Viereck and Little 1972; Smithberg 1974; McLean 1979). Conway (1949, cited by Smithberg 1974) states that red-osier dogwood is able to live with its roots immersed in water. Its presence as an understory species on river floodplains and in wetlands throughout much of B.C. certainly attests to an ability to tolerate flooding.

Light Relations: Rowe (1983) describes red-osier dogwood as semi-tolerant to shade-tolerant, while (Smithberg 1974) states that it is suppressed in shade and thus is never a dominant understory plant. In northcentral B.C., red-osier dogwood is a common understory shrub in relatively open mixed forest and may dominate under aspen or black cottonwood (see e.g., Haeussler *et al.* 1984; Pojar *et al.* 1984) but it rarely displays the vigour that it has at forest margins and in openings. Sheppard and Pellet (1976) studied the effect of a range of light intensities on the growth of red-osier dogwood. Plants grown in full sun were dense and compact with many lateral branches and a high proportion of leaves, while those grown in 27% of full light were open and sprawling with fewer branches and leaves. Shaded leaves were larger, thinner, had less curl and less purple fall coloration than those grown in full light. Flowering was greatest at the higher light intensities. Above-ground biomass was greatest at 75%, but the authors speculated that some moisture stress may have occurred in the 100% light treatment, and that similar stresses might not develop in the wet soils where the shrub is found in nature.

Temperature Relations: The temperature relations of red-osier dogwood have been studied in great detail. Soil temperature affects root and top growth, water usage, and nutrient relations (Barr and Pellett 1972). Optimum root growth occurs between 12 and 26°C, while shoot growth peaks at soil temperatures of 22–29°C. Heavy root mortality occurs at 37°C. Soil temperature has a significant impact on the percentage of phosphorus and potassium in above-ground tissues but no effect on percent nitrogen. Water use increases with soil temperature.

Cold-hardiness of red-osier dogwood is triggered by low temperatures, water stress, and short days (Chen and Li 1978; Bray and Brenner 1980). The degree of cold-hardiness increases steadily as winter progresses, and by the beginning of December most provenances can withstand temperatures from −90 to −196°C. The date at which different provenances of dogwood become acclimated is closely related to the minimum winter temperature and length of growing season in their home territory (Smithberg and Weiser 1968). Once plants become fully dormant, temperatures of 5–10°C or lower are needed to maintain hardiness (Kobayashi *et al.* 1981).

GROWTH AND DEVELOPMENT

Under adequate environmental conditions, early growth of red-osier dogwood is rapid. An average plant can be 1 m tall and put on 1125 cm of branches by the end of the first growing season in the northeastern U.S. (Smithberg and Weiser 1968). Because layering and suckering occur readily, the plant is usually shrubby with many stems. Under intense grass competition, however, layering can be prevented and the species will remain single-stemmed. The form of the plant is also greatly affected by light conditions (see "Light Relations"). Under shady conditions the plant tends to grow into a tall scraggly shrub (Smithberg 1974). Red-osier dogwood varies considerably in height at maturity. In Alaska and Alberta its height typically ranges from 1 to 3 m (Viereck and Little 1972; Watson *et al.* 1980), while at more southerly latitudes, 3 to 5 m is common (USDA 1974; McLean 1979). Heights of up to 9 m have been observed in B.C. (B.M. Geisler, pers. comm., Jan. 1985).

Phenology: Spring phenological events such as bud burst, flowering, and the change of bark colour from red to green are primarily controlled by spring temperatures. The timing of these events varies significantly from year to year depending on weather conditions. In contrast, fall phenological events such as bud set, leaf abscission, bark reddening, and the onset of dormancy, are triggered primarily by shortening daylengths and, within a provenance, they vary little from year to year (Smithberg and Weiser 1968).

The development of dormancy or vegetative maturity in red-osier dogwood has been carefully studied (Seibel and Fuchigami 1978*a*, 1978*b*; Crabtree and Fuchigami 1979; Kobayashi *et al.* 1982).

Red-osier dogwood flowers between May and June in the northeastern U.S. (Smithberg 1974), and in June and July in Alaska (Viereck and Little 1972). Fruits ripen between July and September at both locations. Second flushes of bloom are common in late summer in northeastern U.S. Vegetative phenological events were recorded in the Kimsquit valley on the central B.C. coast during 1983 and 1984 (T.

Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.). Flushing occurred during middle to late April and leaves were fully expanded by mid-May. The first leaves began to turn colour in early August. By mid-September most leaves were coloured; most shrubs retained some leaves until mid-October.

REPRODUCTION

Seed Production and Dispersal: Red-osier dogwood typically bears its first fruit at 3–4 years of age, but yields are light for the first few years (Smithberg 1974). Good seed crops are produced every 1–2 years (Watson *et al.* 1980). The fruit are globular, white drupes with a single two-seeded stone or nutlet. Because the seed is heavy and encased in a fleshy fruit, dispersal is primarily by birds and other animals (Smithberg 1974; USDA 1974), and seeds tend to be located in caches or dropping piles rather than being randomly distributed (Rowe 1983).

Seed Viability and Germination: The seeds remain viable for 4–6years in cold dry storage. The seeds have a 60- to 90-day cold temperature requirement to break embryo dormancy and normally germinate the following spring (Shaw 1984; USDA 1974). However, this is a seed banking species, and seeds can remain dormant for several years until conditions become favourable for germination (Smithberg 1974; Rowe 1983). Germination of the stored seed is favoured by light fires of short duration that partially remove the organic layer (Rowe 1983). Germination appears to be best when seeds are buried slightly beneath the soil surface (Watson *et al.* 1980).

Vegetative Reproduction: Red-osier dogwood develops into dense thickets through vegetative propagation. As its alternative scientific name (*C. stolonifera*) indicates, red-osier dogwood is capable of producing stolons or prostrate above-ground stems that root at the nodes and send up new shoots. Smithberg (1974) indicates that this form of reproduction was observed most often on very moist or wet sites. The stolons can extend as far as 3 m from the parent plant (B.M. Geisler, pers. comm., Jan. 1985). Other forms of vegetative reproduction include layering of branches that come into contact with the soil; suckers that develop from dormant buds in the roots; and sprouts from old branches or stem bases. Cuttings of red-osier dogwood root very successfully (Marchant and Sherlock 1984).

PREDATION AND PESTS

Red-osier dogwood is a major winter browse species for moose, a preferred food of deer, and is also browsed by elk, mountain goats, black bear, snowshoe hare, beaver, and many other mammals. The fruit are eaten by 93 different bird species and are a favourite fall food of ruffed grouse (Smithberg 1974).

EFFECTS ON CROP TREES

Competition: Throughout B.C., red-osier dogwood can be a significant competitor with coniferous trees on subhygric to hydric sites that have a well-established, diverse brush community. These sites are often very productive for tree growth. Red-osier dogwood has an advantage of being established prior to harvest and can form a dense thicket. There is no published information regarding the effect of red-osier dogwood on the growth of crop trees.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: There are few data to indicate how red-osier dogwood responds to logging. Eis' study (1981) shows that 6 years following canopy removal, *C. sericea* was still present but had not become a dominant species on any of four different site types in the SBS zone north of Prince George. Harcombe *et al.* (1983) indicate that removal of the tree canopy will enhance red-osier dogwood, especially near wetter areas.

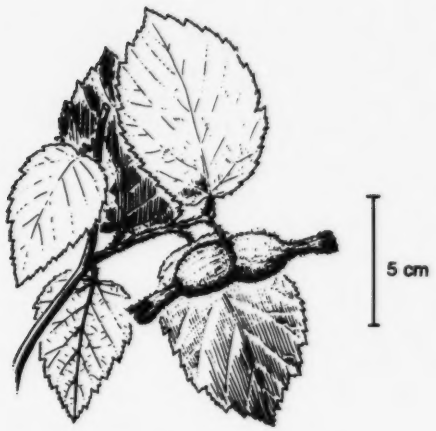
Fire: Rowe (1983) indicates that light fires stimulate germination of stored seed of red-osier dogwood. Response of the mature plant to fire is unstudied.

Cutting: Clipping produced a slight increase in total twig production of red-osier dogwood, but under heavy browsing, this species becomes spiny and its growth is retarded (Aldous 1952).

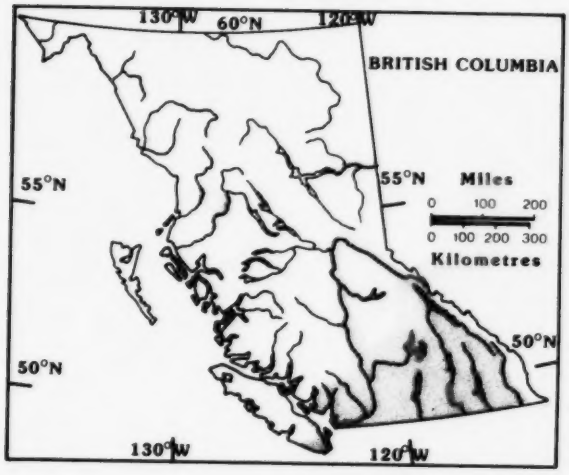
Herbicides: Spraying with 2,4-D or paraquat prior to vegetative maturity caused tip die-back, damaged foliage and delayed spring budbreak and growth in Oregon (Crabtree and Fuchigami 1979). The effect of the

herbicides was reduced when plants were sprayed following vegetative maturity. The authors recommended that the species be sprayed prior to the onset of vegetative maturity for maximum effectiveness, and they are developing a field test to determine when this stage (which precedes visible leaf senescence) is reached. Red-osier dogwood appears to be quite tolerant of glyphosate (Expert Committee on Weeds 1984).

Soil Disturbance: Buried stem fragments of red-osier dogwood root readily without any special treatment in moist or wet soil. Plant parts are especially prone to rooting when they are cut during the dormant season (Smithberg 1974). Plants damaged during mechanical site preparation can be expected to sprout or sucker from roots and stem bases. Exposure of mineral soil may stimulate germination of buried seed.



Corylus cornuta (hazelnut).



Distribution of *C. cornuta* in British Columbia.

Corylus cornuta Marsh. — Hazelnut

(beaked hazelnut, beaked filbert)

DESCRIPTION

Hazelnut is a deciduous, multistemmed shrub up to 4 m tall. The shrub can be densely clumped or widely spreading by means of underground stems. Twigs are brown to orange, with hairy buds. Leaves are soft and hairy, more-or-less round with sharply toothed margins. Male catkins appear before the leaves in early spring; female flowers are inconspicuous with protruding stigmas. The fruit is a round hazelnut enclosed in a hairy husk with a pronounced beak (Tappeiner and John 1973; Brayshaw 1978).

Variation: There are two varieties of *C. cornuta* in British Columbia. *Corylus cornuta* var. *cornuta* is found across northern North America but is absent west of the Coast Mountains. It is replaced on the Lower Mainland and Vancouver Island by var. *californica*, a taller, clumped shrub with darker twigs and broader leaves. Introgression between the two varieties occurs in southern B.C. (Taylor and MacBryde 1977; Brayshaw 1978). The cultivated hazelnuts commonly planted in southwestern B.C. are not included in this discussion.

DISTRIBUTION AND ABUNDANCE

Hazelnut is found in major valleys throughout southern B.C. and on southeastern Vancouver Island. It extends north to Prince George and McBride following the Fraser River, and there are populations in the Peace River valley and in the Coast/Interior transition in the Skeena and Nass valleys. It is found primarily in the ICH zone and drier CWH subzones, but also occurs to some extent in the IDF, southern SBS, and BWBS. Hazelnut has a discontinous distribution throughout its range in B.C. and tends to be abundant only in localized areas. It is absent from subalpine areas and from the driest valleys of the southern Interior.

Altitudinal Range: Hazelnut is found primarily at low elevations. It ranges from sea level to 800 m on the south Coast, to 1200 m at Revelstoke (Lyons 1952), and to approximately 750 m in the Skeena Valley (Haeussler *et al.* 1985)

HABITAT

Climatic Relations: The range of *C. cornuta* in North America implies that this species is not well adapted to high summer temperatures nor to the extreme northern boreal climate (Stearns 1974). In B.C. it tends to be found in rainshadow areas on the Coast, in subcontinental or Coast/Interior transitional climates, and in moist, but not wet, climatic areas of the southern Interior. This distribution suggests that it is not adapted to heavy rainfall, nor to a harsh, droughty or snowy environment. The var. *californica* apparently favours a mild, equable climate, while var. *cornuta* is adapted to more continental conditions.

Site and Soil Conditions: Throughout most of North America, hazelnut is found in open woods, thickets, pastures, and clearings. It favours well-aerated, loamy soils over organic or gleysolic soils, and does poorly on heavy clay soils or excessively coarse sandy soils (Stearns 1974). Lyons (1952) states that it is equally at home on exposed rocky sites and in shady glades. It is common on open floodplain sites in Oregon (Hawk and Zobel 1974) and is abundant and vigorous on fluvial parent materials in the Skeena-Nass area (Haeussler *et al.* 1985).

Nutrient Relations: In Minnesota, *C. cornuta* is found on soils with pH values ranging from 5.3 to 6.1 (Hsuing 1951, cited by Stearns 1974). Ecosystem associations in which hazelnut is a dominant understory species are generally characterized as moderately rich (mesotrophic - permesotrophic) to very rich (eutrophic) in nutrients (see e.g., Haeussler *et al.* 1985; Utzig *et al.*[37]). Tappeiner and John (1973) estimated the nutrient concentrations and total nutrient content of *C. cornuta* understories in northern Minnesota pine stands. Compared to the overstory, hazelnut appeared to be rich in calcium, phosphorus, and magnesium. It contained from 2 to 22% of the nutrients in above-ground vegetation, even though it was only 5% of the above-ground biomass.

Water Relations: *C. cornuta* favours sites that are moist but well drained, and it does not grow well on wet, poorly aerated sites (Stearns 1974). Krajina *et al.* (1982) report that the species grows on sites with a mesic to hygric moisture status, and has a high tolerance of flooding.

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[37] G. Utzig, D. MacDonald, and P Comeau. 1978. Ecological classification for the Nelson Forest District. Second approximation. B.C. Min. For., Nelson, B.C. Unpublished report.

Light Relations: Stearns (1974) indicates that *C. cornuta* requires 30% or more of full sunlight for best growth and will not germinate or grow well in dense shade. In B.C., hazelnut occurs primarily in the understory of open deciduous or mixed stands or in forest openings (Haeussler *et al.* 1985; R. Coupé and R.M. Mitchell, pers. comm., Nov. 1984).

Temperature Relations: Krajina *et al.* (1982) indicate that frost resistance is probably high, but note that its habitats probably afford hazelnut some protection from frost. The *var. cornuta* undoubtedly has a higher frost resistance than var. *californica*.

GROWTH AND DEVELOPMENT

Hsuing (1951, cited by Stearns 1974) has conducted an in-depth study of the growth of seedlings and clones of *C. cornuta* in Minnesota. Most of the following information was taken from Hsuing's study and it probably applies well to the growth of beaked hazelnut in the Interior of B.C. Variety *californica* is known to have a different pattern of growth. It is a taller shrub, reaching 4 m or more at maturity, and does not expand by suckering (Brayshaw 1978; M. Newton, pers. comm., Dec. 1984).

Following germination from seed, hazelnut produces a deeply penetrating taproot. If growing conditions are favourable, a vigorous system of tap and lateral roots will develop. When the seedling is 7- to 12-years-old, it starts to develop underground stems. The lateral roots and underground stems of hazelnut occur in the uppermost 20 cm of the soil, often at the boundary between humus and mineral soil.

A young plant grown from seed sprouts from dormant buds only after damage to the main stem. Once the plant is well established the rate of sprouting increases. Vigorous stems can reach heights of 60 cm or greater in 2 years. In Manitoba, untreated hazelnut grew an average of 43 cm, from 1.2 to 1.6 m tall, in six growing seasons (Waldron 1959). Individual branches can live for more than 18 years and the plant itself survives for an indefinite period of time. At 15–20 years the average height is 2.5 m, but as the stem becomes overmature, growth declines. Decadent stems often grow only a few centimetres per year.

Hazelnut has a very dense, multilayered canopy that allows little light to penetrate. Total leaf area over a 0.4-ha plot equalled 2.8 ha (Waldron 1959). Because it produces underground stems, hazelnut has a relatively large proportion of its biomass (31–39%) undergound (Tappeiner and John 1973).

The rate of spread of clones is slow but increases with age. A 6-year-old clone had one to two shoots and was 2 cm in diameter at the base. By 38 years of age it was 250 cm in diameter and had 25 shoots. Size and vigour of the shoots increases with the size and age of the clone.

Phenology: Male catkins are evident as elongate buds the year before flowering. Female buds are less evident. Both male and female flowers emerge before the leaves, during March and April in the northeastern U.S. (Stearns 1974). In Oregon, male catkins were fully expanded but unopened by 17 March (Stewart 1974*b*). Fruits ripen during August and September in B.C. (Brayshaw 1978).

Stewart (1974*a*, 1974*b*) reports the following sequence of vegetative development for *C. cornuta* in coastal Oregon: vegetative buds were swelling but closed on 17 March; by 16 June, three quarters of the leaves were fully developed; and by 11 August all vegetative growth had ceased.

REPRODUCTION

Seed Production and Dispersal: Male and female flowers are borne separately on 1-year-old twigs of the same plant. They are formed late in summer and open prior to the leaves the following spring. Fertilized female flowers develop into round, hard-shelled nuts (USDA 1974). Production of flowers depends on weather, site, and light conditions. Late frosts can kill flowers and dry weather can affect fertilization (Hsuing 1951, cited by Stearns 1974).

Production of fruit increases with stem age, peaking at 10–11 years and ceasing when twigs are approximately 18 years old. There can be large fluctuations in fruit production from year to year, and good crops occur approximately once in 5 years. Production rates vary from approximately 32 000 nuts per hectare to as low as 100 per hectare with as many as six to eight nuts per branch in good seed years (Stearns 1974).

Dispersal of the heavy seeds is primarily by small mammals such as squirrels and chipmunks and some birds.

Seed Viability and Germination: Actual survival of seeds is low because so many nuts are destroyed by predators (Stearns 1974). The seeds have poor viability in storage and must remain moist. Two to six months of chilling are required before germination can take place (USDA 1974). Germination rates are quite poor, averaging 30–60% in laboratory tests. Best germination occurs when nuts are covered to prevent drying out (Stearns 1974). Hsuing (1951, cited by Stearns 1974) obtained 30% germination in an upland soil, 56% on a black spruce - tamarack site, and 0% in a wet swamp in Minnesota. Although few nuts actually produce seedlings, in good seed years spread by seed is a major factor enabling hazelnut to invade new areas.

Vegetative Reproduction: Vegetative reproduction from underground stems is by far the most important means by which hazelnut colonizes a site (Ahlgren 1960; Buckman 1964). Horizontal stems radiate outward from the parent plant just beneath the litter layer. Rooting occurs along the length of the underground stem, and aerial shoots arise at scattered locations to produce new plants (Tappeiner and John 1973; Brayshaw 1978). In many areas of North America the clones of *C. cornuta* var. *cornuta* become larger and larger until they eventually grow together, forming a continuous shrub layer (Buckman 1964; Tappeiner 1971). *Corylus cornuta* var. *californica* apparently does not produce large clones but tends to remain as a compact shrub or small tree (Brayshaw 1978). Other methods of vegetative reproduction common to both varieties of hazelnut include vigorous resprouting of cut stems, layering of aerial branches buried in soil, and artificial rooting of cuttings (USDA 1974).

PREDATION AND PESTS

Hazelnut is browsed by moose, deer, and snowshoe hare, but is not considered to be a preferred browse species. Birds consume the buds and catkins. The hazelnuts are a valued food of many small rodents, particularly squirrels and chipmunks, as well as some birds (Stearns 1974). Squirrels have been known to consume entire crops of hazelnuts, often before they are ripe (USDA 1974), and a single red squirrel in Alberta can consume as many as 80 hazelnuts in one day (Stearns 1974).

EFFECTS ON CROP TREES

Competition: In B.C., hazelnut is not considered to be a major brush species because it is mostly abundant in valley bottom areas that are removed from forest production either by land alienation or because they have long been dominated by non-commercial hardwood species (R. Coupé and W.R. Mitchell, pers. comm., Nov. 1984). However, many sites with an understory of hazelnut are highly productive and could be considered for conversion to coniferous species.

In other areas of North America hazelnut is a very aggressive competitor, and a major deterrent to successful regeneration of upland conifers. Dense aerial stems of hazelnut inhibit the establishment of natural regeneration of conifers and other shrub species (Tappeiner 1979). The primary impact of hazelnut on conifers is believed to be shading, caused by its aggressive growth and densely layered canopy (Waldron 1959; Buckman 1964). Available light may only be 2–7% of full sunlight beneath a dense canopy of hazelnut (Stearns 1974). The extensive and shallow root system can also cause severe competition for moisture in upper soil layers (Stearns 1974). Tappeiner and John (1973) also indicate that dense shrub layers of hazelnut tie up a significant component of total site nutrients in their above-ground biomass.

Beneficial Effects: Although hazelnut biomass may tie up a significant quantity of nutrients, these nutrients are recycled through the ecosystem, where they can become available to coniferous trees. Tappeiner and Alm (1972, cited by Tappeiner and John 1973) showed that in jack pine stands with hazelnut present in the understory, total macronutrients present in the litter were nearly double the amount present in pure pine litter.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: The increased light reaching the forest floor after logging of spruce or after mortality of decadent aspen results in rapid expansion of established hazelnut colonies (Hsuing 1951, cited by Waldron 1959). Reduction of overhead competition increases stem vigour and stimulates both fruit and vegetative growth (Stearns 1974).

Fire: In most situations, hazelnut responds vigorously to fire. Above-ground parts are immediately killed, even after a light spring fire, but the shrub responds by sprouting prolifically from stem bases and sending up new

aerial shoots. The original stand is replaced in stature and number of stems in only a few years (Ahlgren 1960; Buckman 1964; Wright 1972). The establishment of continuous colonies of hazelnut in some areas of B.C. is probably the result of recurrent fires over a lengthy period of time.

However, because underground stems and roots are located just beneath the humus layer, burning can eradicate hazelnut if burns are carried out when the humus is dry and combustible. Repeated spring burning, done when the soil is moist, simply increases the number of stems present; but a series of burns carried out in midsummer can cause hazelnut to decline in vigour and abundance by consuming the protective layer of humus and exhausting stored food reserves. If a stand of hazelnut is in the early stages of development with scattered clones rather than a continuous canopy, hazel can be controlled with as few as two summer burns (Buckman 1964; Tappeiner 1979).

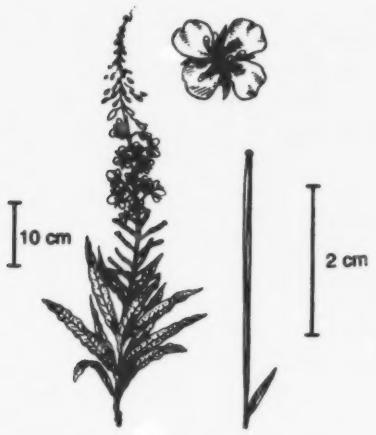
Cutting and Browsing: Heavy browsing by deer can stimulate hazelnut to produce basal sprouts or suckers (Stearns 1974). A clipping experiment by Aldous (1952) produced similar results. Total twig production was increased for 3 years under heavy clipping, but thereafter began to decline. Light clipping had little impact on growth.

Herbicides: 2,4-D produces heavy top-kill in hazelnut, but resprouting can be vigorous (Ahlgren 1960; Sutton 1958; Waldron 1959; Tappeiner 1979). Waldron (1959) found that resprouting was delayed for 2 years following a midsummer foliage spray. Six years later there were 67–85% as many stems as on the control and stems were 30–60 cm shorter. Stewart (1974*a*) suggests that an early foliar spray may be most successful in controlling resprouting in Oregon, but Tappeiner (1979) found that Minnesota hazelnut was more tolerant in June than in July or August.

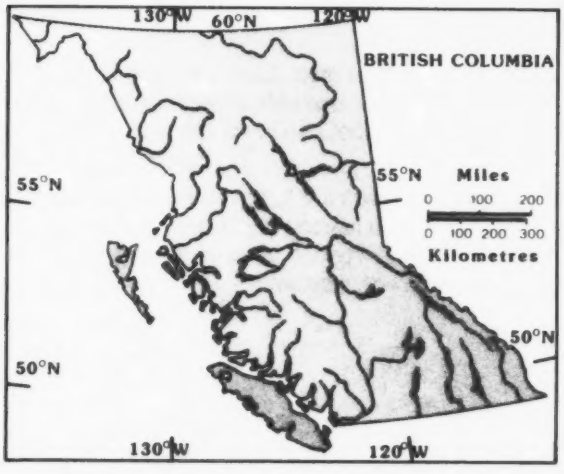
In Ontario, glyphosate applied in late August was highly effective in killing hazelnut at rates of 2.24 kg ai/ha and greater (Sutton 1978). Conard and Emmingham (1984*a*, 1984*b*) report that glyphosate applied in the spring, late summer, or fall causes severe (60–90%) or very severe (90–100%) injury to hazelnut in Washington and Oregon.

Perala (1971) found that picloram was much more effective than 2,4-D or a 2,4-D/2,4,5-T mixture in reducing resprouting of hazelnut in Minnesota. Average recovery after 2 years was less than 10%. Aerial spraying was less successful than backpack spraying. Conifers were damaged by most applications and the site was invaded by grasses and sedges.

Soil Disturbance: Disk site preparation of a hazelnut brushfield in midsummer turned up the underground stems and set growth back for several years (Eyre and Zehngraff 1948, cited by Ohmann 1982). As long as underground stems are not destroyed or removed during mechanical site preparation, hazelnut will sprout back and the number of aerial stems will be increased in the long run (Stearns 1974).



Epilobium angustifolium (fireweed).



Distribution of *E. angustifolium* in British Columbia.

Epilobium angustifolium L. — Fireweed
(Chamaenerion angustifolium)

DESCRIPTION

Fireweed is a tall herbaceous perennial that forms extensive colonies through a spreading system of fleshy roots or "pseudorhizomes". The root system gives rise to erect, usually unbranched annual shoots 1–3 m tall. The untoothed, linear to lanceolate leaves are spirally arranged around the stem. Each stem has a large, showy terminal cluster of pink to purple flowers. The fruit is a narrow capsule up to 10 cm long, that releases large numbers of plumed seed (Mosquin 1966; Myerscough 1980).

Variation: *Epilobium angustifolium* is a completely circumpolar species with two recognized subspecies (Myerscough 1980). Both subspecies occur in British Columbia. The diploid ssp. *angustifolium* is found in the northern boreal forests and at high elevations in the mountains, while ssp. *circumvagum* occurs at lower elevations in south and central B.C. The latter subspecies has larger leaves and is generally taller and coarser than ssp. *angustifolium*. There is considerable intergradation where these two subspecies overlap (Mosquin 1966; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Fireweed is one of the most widely distributed of all plant species (Mosquin 1966). It is found throughout B.C. and occurs in all biogeoclimatic zones wherever soil moisture is sufficient (McLean 1979). Fireweed is extremely common and abundant throughout the central and northern Interior of B.C., but is more scattered on the outer Coast (J. Pojar, pers. comm., Oct. 1984) and in the dry southern Interior (Angove and Bancroft 1983).

Altitudinal Range: In B.C., fireweed ranges from sea level to high alpine meadows. It has been found at elevations as high as 4000 m in the mountains of western North America (Mosquin 1966).

HABITAT

Climatic Relations: The extremely broad range of this species indicates that it can tolerate a wide range of climatic extremes. In northern climates the species appears to be confined to warm sunny locales and south-facing slopes; towards the central portion of its range, including B.C., it occurs on a wide range of slopes and aspects; at the southern end of its distribution, in hot, dry climates, it favours cool, moist, shaded locales and high alpine and subalpine habitats (Myerscough 1980). Mosquin (1966) indicates that at the northern limits of the range of fireweed in Canada, plants are frequently sterile.

Site and Soil Conditions: Fireweed tolerates a very wide variety of soil and site conditions (see e.g., Myerscough 1980 for Britain), but is most commonly associated with disturbed sites such as logged, windthrown or slashburned areas (Dyrness 1965; McLean 1979), recently deglaciated terrain, or mine wastes (Watson *et al.* 1980).

Epilobium angustifolium also occurs in mature, usually seral, forest ecosystems in the Interior of B.C. (see e.g., Pojar *et al.* 1984), and is common in undisturbed alpine and subalpine meadows (Mosquin 1966). Fireweed occurs on organic soils, but also on soils with little or no organic matter. It is found on virtually all different kinds of parent material, and on a wide range of soil textures, but is most common on sandy loam to loamy soils (Myerscough 1980).

Nutrient Relations: Fireweed can tolerate a wide range of pH values (pH 3–9) and nutrient concentrations (Myerscough and Whitehead 1967; van Andel 1976; van Andel *et al.* 1978; Myerscough 1980). It is frequently reported to be a nitrophilous (nitrogen-demanding) species, or at least an indicator of nitrogen-rich habitats (Buesgen and Muench 1929, cited by Taylor 1932; Tamm 1956). However, experiments by van Andel (1976) suggest that while the plant has great adaptability to high levels of nitrogen, potassium, phosphorus, and calcium, it does not appear to depend on them. These results from Europe correspond with observations and experimental results from western and northern Canada. Fireweed is frequently an invader of bare till and nitrogen-poor mining wastes, as well as sites with a post-fire "nutrient flush" (Watson *et al.* 1980). In the SBS zone north of Prince George, fireweed occurred on sites with an extremely wide range of available calcium (Wali 1969). Plants growing where the mineral nutrient supply is low may not produce flowers (van Andel and Vera 1977).

Water Relations: Myerscough (1980) reports that *E. angustifolium* occurs most commonly on soils that are at least freely drained, but that it occasionally occurs in waterlogged mires. Over much of B.C. it tolerates a wide range of moisture conditions (Pojar *et al.* 1982; Angove and Bancroft 1983), but appears to have best growth on subhygric to hygric seepage sites.[38] Towards the northern limits of its range it apparently becomes less tolerant of excessive moisture and may be restricted to well-drained soils only (Myerscough 1980). The plant is known to tolerate rather dry sites but can not germinate in droughty conditions (Watson *et al.* 1980).

Light Relations: As a plant associated with the pioneering stages of succession and most often seen on open ground, fireweed is presumably somewhat light-demanding (Watson *et al.* 1980). Flower buds form earlier in unshaded colonies than in shaded ones and in deep shade the plant does not flower (Myerscough 1980). In intermediate shade and full sun, plants have roughly equivalent growth rates, but in deep shade growth rates are much reduced and seedlings are etiolated (Myerscough and Whitehead 1967).

Temperature Relations: The range of this species suggests that it is adapted to survive and grow under a variety of temperature regimes. Under experimental conditions, roots initiated growth at 4.5°C, while shoot growth occurred only at higher temperatures (Myerscough 1980). Emergent shoots tolerate some frost in spring but may later show minor tissue damage.

GROWTH AND DEVELOPMENT

Under favourable environmental conditions, fireweed seedlings grow at a comparatively rapid rate for the first 5 weeks from seed. Seedlings that germinate in late summer or early fall occasionally overwinter as a small rosette of evergreen leaves, but spring germinants may reach a mature height and produce flowers during their 1st year of growth (Myerscough 1980).

The seedling quickly develops an extensive root system. Shoot buds are produced along the length of the root system, giving rise to a colony of plants. These shoots expand late in the growing season and overwinter just beneath the soil surface (Myerscough 1980). In the spring, they emerge from the soil to form the erect annual shoots. Aerial shoots normally exceed 1 m in height at maturity, but height growth seems to be strongly correlated to environmental conditions, and best growth is generally observed on moist, subhygric sites under full light conditions. Up to 120 shoots per square metre have been observed in some populations, and emergent shoots may reach a maximum biomass of 600–900 g/m^2 (van Andel 1975).

Myerscough (1980) states that the fleshy underground roots of fireweed are most abundant at 5–20 cm below the soil surface and can penetrate deeper than 40 cm, but this does not appear to be the case in southern B.C., where McLean (1969) found most roots located between 1.5 and 5 cm beneath the soil surface. Lateral spread of a colony of fireweed averaged 1 m per year over several years (van Andel 1975). There is no information regarding how large a colony can become, but field populations have a longevity of several decades, and the roots can live for over 20 years (Moss 1936; van Andel 1975).

The development of a population of *E. angustifolium* along a roadside in Britain was studied for 20 years (Myerscough 1980). There was a progressive increase in above-ground biomass of the colony for the first 7 years, with the population remaining fairly stable for 12 years, followed by a rapid decline in biomass as die-back occurred. Development of fireweed stands may be quite different in many areas of B.C. because succession proceeds too rapidly to allow pioneer conditions favourable to fireweed to persist for as long as 20 years. In the CWHa subzone, for example, fireweed appears to reach its peak dominance in the second or third growing seasons following disturbance, and subsequent in-growth of shrubs and trees is rapid.[39] Once a forest canopy develops, fireweed generally dies out, but it can persist at low densities and vigour in the understory of open stands in Interior B.C. (Mosquin 1966; Pojar *et al.* 1984).

Phenology: Roots begin growing before shoot buds below the surface begin to elongate. Aerial shoots first begin to emerge anywhere from late March to early June at mid-latitudes, but most emerge in May. Leaves are full grown approximately 1 month later and maximum biomass is reached between the middle of June and the end of August. Aerial shoots begin to wither in late July or early August and all have died back by late September or early October (Myerscough 1980; Schmidt and Lotan 1980).

[38] Brand, 1984.
[39] Ibid.

The flowering season extends from June to September because the inflorescence begins to flower at the base and continues to elongate during the summer, producing blossoms at the tip of the plant long after the basal fruits have ripened and released their seed (Clark 1976). In the intermountain U.S., seed ripening begins in late July (Schmidt and Lotan 1980). Seeds are released throughout the late summer until after the aerial shoots have withered in autumn.

REPRODUCTION

Seed Production and Dispersal: The plants can flower in their 1st year of growth from seed. The flowers are noted as nectar producers and thus are sought out by bees, butterflies, and other insects. Production of seeds is usually copious in temperate environments. There are an estimated 250–500 seeds in each capsule, and estimates of production for each live stem range from 20 000 to 80 000 or higher. The plumed seeds are dispersed by the wind, and they are very slow to settle (Salisbury 1961; Mosquin 1966; Myerscough and Whitehead 1966; Myerscough 1980). Fireweed accounted for 63% of the seed obtained in seed traps 1 year after fire at a northern Saskatchewan site (Archibold 1980). This represented 5.66 million seeds per hectare.

Seed Viability and Germination: Seeds of fireweed normally lose their viability after 18 months, but germination continues at reduced rates for up to 2 years. Although, seeds are capable of germinating immediately on release, best germination rates may occur approximately 3 months after dispersal. Germination is stimulated by light, a chilling period, and treatment of the seed in dilute acid (Myerscough 1980).

Seedlings germinate most often in late summer or early autumn following summer fires, or they may germinate the following spring. Germination appears best between 15 and 35°C. Only seeds on or near the soil surface germinate successfully. Germination is most successful on moist, open sites with few initial plant competitors. Fertilizing sites with poor nutrient status also seems to improve germination (Myerscough and Whitehead 1966, 1967; Myerscough 1980).

Archibold (1980) found viable buried seed in soil cores taken immediately following a fire in northern Saskatchewan. He speculates that seed banking may account for the rapid invasion of fireweed on burned sites. Given the short viability of fireweed seed, it does not seem likely that large quantities of seed could become buried in the forest floor at a depth sufficient to survive a forest fire.

Vegetative Reproduction: Fireweed relies on large quantities of seed to colonize disturbed areas, but once it arrives on a site, expansion of the population is accomplished by vegetative reproduction. New shoots arise each year from buds located at the base of old stems, and on the horizontally spreading root system 2–8 cm below the soil surface. The root system is perennial and with each year it spreads further outward from the original seedling. New plants are created when they become detached from the parent plant through death of old roots or through disturbance. In an established colony of fireweed, vegetative reproduction has clear priority over reproduction by seed (Moss 1936; Myerscough 1980).

PREDATION AND PESTS

Fireweed is grazed by cattle, elk, deer, and moose (McLean 1979; Watson *et al.* 1980). Grazing occurs throughout the growing season but particularly when plants are in flower (McLean 1979). Small mammals use fireweed seed (Watson *et al.* 1980). Myerscough (1980) provides a comprehensive list of the many insects and diseases found on *E. angustifolium* in Britain.

EFFECTS ON CROP TREES

Competition: Fireweed is considered to be a species of low competitive ability because it is a pioneer of recently disturbed sites and will not invade sites with previously established vegetative cover (Mosquin 1966; Watson *et al.* 1980). It is nonetheless a significant competitor with coniferous trees in the early stages of stand establishment.

Fireweed is generally considered to be of secondary importance as a competitor with coniferous seedlings, despite its widespread abundance. It is short-lived and low-growing compared to many woody brush species. In addition, competition for light is relatively minor because the aerial shoots must grow from the ground up each spring, and the mature fireweed canopy allows considerable light to penetrate (Eis 1981).

Fireweed is of more concern in the central and northern areas of the province than on the south Coast because it is more ubiquitous, and the slower-growing seedlings may be overtopped by fireweed for 10 or more years following establishment. On the south Coast, succession also proceeds more rapidly and fireweed is outgrown by more competitive woody brush within 1–3 years,[40] whereas in the Interior, an early successional stage dominated by fireweed can persist for a decade or more.

Throughout B.C., fireweed damages young seedlings primarily through snowpress by dead annual shoots (Brand;[41] J. Pollack, pers. comm., Jan. 1985). Douglas-fir is particularly susceptible to this type of damage because young seedlings are very flexible and lacking in caliper (D. Lloyd, pers. comm., Nov. 1984). Root competition for soil moisture and nutrients is also significant.

Beneficial Effects: An important beneficial effect of a cover of fireweed is that it may delay development of shrubby vegetation on cleared or burned areas (see e.g., Stickney 1981), thus allowing planted conifers to gain dominance of a site once they outgrow the fireweed. Its extensive root system helps to bind soil and reduce erosion (Watson *et al.* 1980). Invasion by fireweed undoubtedly increases the organic matter content of severely burned or otherwise disturbed sites.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Fireweed agressively colonizes logged-over areas (Mosquin 1966). Colonization is achieved primarily by seeding-in, but where fireweed already exists prior to canopy removal, it is able to expand by means of its spreading root system (McLean 1979; Myerscough 1980; Rowe 1983).

In Eis' study (1981) of four site types in the SBS zone north of Prince George, fireweed was absent from all sites prior to logging. He observed that fireweed's "first few seeds arrive in the fall of the first year following winter logging and germinate in the spring of the second year. Its presence is most noticeable during the third year after logging and . . . it appears in great numbers during the fourth year." Six years after logging, fireweed accounted for greater than 60% of the herbaceous ground cover on the Cornus-Moss type and 50% on the Dryopteris-Aralia, but was less than 20% of the cover on the Devil's club site and was not a significant competitor on the Alluvium site. This study demonstrates that fireweed is able to rapidly exploit a vacant niche but is unable to compete where vegetation is already well established. The Cornus-Moss type had a low diversity and cover of vegetation immediately after logging and fireweed readily became dominant. In contrast, shrubs and herbs were already well established on the Alluvium site and fireweed was unable to move in.

Fire: Fireweed is well known in western North America for its ability to invade recently burned areas (Mosquin 1966; Dyrness 1973; Watson *et al.* 1980; Stickney 1981). Its light seeds rapidly colonize vacant ground space following a burn, and it can form dense, uniform stands over vast areas. It favours burned ground over unburned ground, and density is greatest on the areas that suffer the hardest burn (Ahlgren 1960; Mueggler 1965; Morris 1970). Tiedemann and Klock (1974) observed that fireweed increased in cover for the first 2 years following a burn in eastern Washington, then remained static. On moist, rich sites in the CWH zone near Vancouver, fireweed was absent during the first growing season but was abundant 2–4 years after burning.[42]

McLean (1968) classified fireweed as moderately susceptible to fire because its fibrous roots are mostly located within the upper 5 cm of the mineral soil surface. Fireweed rapidly loses vigour and will not survive under regimes of regular frequent burning (Myerscough 1980); however, it has a very low flammability and can suppress fire in early successional vegetation types where it is abundant. The plant acts as a heat sink because of its high moisture content and there is little standing dead fuel because its litter decomposes rapidly (Sylvester and Wein 1981).

Cutting and Grazing: There are no reports in the literature describing the response of fireweed to manual cutting. Impact is expected to be short-lived and minimal unless cutting is repeated within a short period of time. Fireweed does not survive continued grazing (Myerscough 1980).

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[40] Brand, 1984.
[41] Ibid.
[42] Ibid.

Herbicides: Two years after glyphosate was applied with a Micron Herbi at 0.5 kg a.i./ha near Blue River, B.C., the majority of fireweed shoots were dwarfed and deformed.[43] Near Prince George, fireweed was reduced by 71% in both cover and height one growing season after glyphosate was applied at 2.25 kg/ha (Expert Committee on Weeds 1984). The results of hexazinone, applied as a liquid at rates of 2.2–4.3 kg/ha, have ranged from nearly complete control to little control (Expert Committee on Weeds 1984).

Soil Disturbance: Fireweed is known to rapidly invade exposed mineral soil and peat (Watson *et al.* 1980), and it is widespread on roadcuts throughout central and northern B.C. It was not abundant on two sites in the CWH zone near Vancouver that were scarified after logging.[44] In the Gaspé Region of Quebec, Mosquin (1966) observed that fireweed was growing poorly on exposed subsoil, but had very good vigour on adjacent sidecast mounds of humus and topsoil.

Fertilization: Fireweed may increase in abundance where fertilizers have been used in silviculture (Reinikainen 1964, cited by Myerscough 1980). Germination is improved on fertilized sites (Myerscough and Whitehead 1967).

Other: Areas seeded to grass can have lower cover and frequency of fireweed than unseeded areas (Hernandez 1973, cited by Watson *et al.* 1980; Crane *et al.* 1983).

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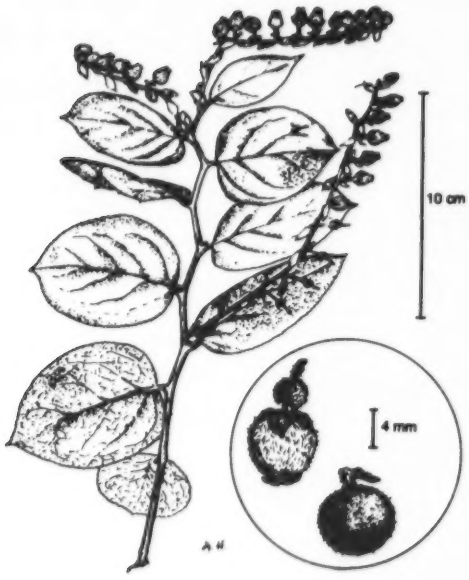
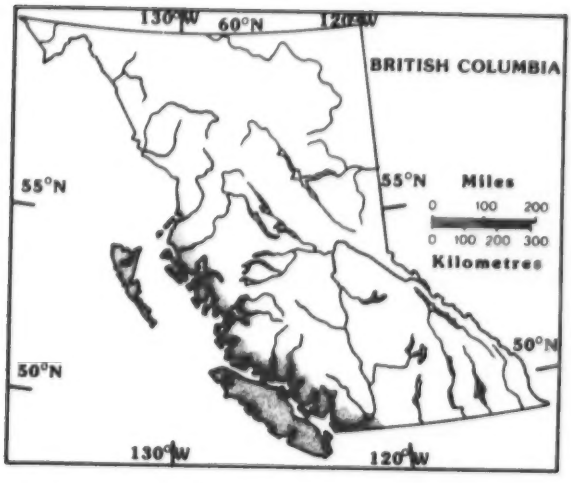
[43] Whitehead *et al.*, 1982.
[44] Brand, 1984.



Gaultheria shallon (salal).



Distribution of *G. shallon* in British Columbia.

Gaultheria shallon Pursh. Salal

DESCRIPTION

Salal is an erect to nearly prostrate evergreen shrub, loosely to densely branched, and up to 2.5 m tall, sometimes forming impenetrable thickets. It has an extensive, shallow root system with spreading rhizome-like structures. The leaves are thick, leathery and ovate, often with finely toothed margins. The pinkish, bell-shaped flowers are borne in terminal and subterminal, one-sided racemes. The fruit is a round, hairy, purplish black, berry-like capsule (Szczawinski 1962; UBC Bot. Garden 1970).

Variation: No subspecies or varieties of salal are described in British Columbia (Taylor and MacBryde 1977). The presence of altitudinal ecotypes is possible, but not probable, and the species apparently does not hybridize (Pojar 1974).

DISTRIBUTION AND ABUNDANCE

Salal occurs along the entire length of the B.C. coast in the CWH, CDF, and CCPH zones, seldom penetrating far inland. A single isolated population of the species is recorded from the Kootenay Lake area, but otherwise all records are from west of the Coast Mountains (Szczawinski 1962). It is extremely abundant in south coastal B.C. but becomes less important on the mainland and inner islands of the north Coast where it is rarely found at any distance from the shoreline.

Altitudinal Range: Salal is primarily a low-elevation species, becoming more restricted in elevation with increasing latitude. On the south Coast it ranges from sea level to approximately 800 m (Lyons 1952), but on the north Coast it rarely occurs above 100–200 m elevation.

HABITAT

Climatic Relations: The restricted range of salal suggests that it requires a humid to perhumid coastal climate with mild temperatures, little snow, and unfrozen soils in winter. In B.C., salal is most vigorous and abundant on Vancouver Island and adjacent coastal areas where the climate is particularly equable.

Site and Soil Conditions: Salal is a dominant understory plant in lowland coniferous coastal forest and is very abundant in open, shoreline habitats such as bluffs and rocky knolls (Calder and Taylor 1968). It grows on a wide variety of mineral and organic substrates including shallow rocky soils, sand dunes, glacial till, and peat. Soils supporting salal are most often Podzols, frequently with deep mor humus forms, but may also be brunisolic, folisolic, and organic soils (see e.g., Klinka *et al.* 1979; Banner *et al.*[45]).

On poor, shallow soils the plants often exhibit a low mat-forming habit, while on better deeper soils they become vigorous upright shrubs (UBC Bot. Garden 1970; M. Newton, pers. comm., Dec. 1984). Best growth in cultivation occurs on moist sandy or peaty soil. Salal frequently grows on decaying wood, particularly old stumps, and in extremely humid environments it can be found as an epiphyte on living trees (UBC Bot. Garden 1970).

Nutrient Relations: Salal can survive and maintain acceptable growth under a wide range of nutrient conditions (Sabhasri 1961). Throughout its range, salal is notable for its abundance in ecosystems considered to have a very poor (oligotrophic — submesotrophic) nutrient status (see e.g., Klinka 1977*a*; Yole *et al.*;[46] Banner *et al.*[47]). Its abundance on these sites reflects a tolerance for nutrient-poor conditions, but should not be construed as a preference for a low-nutrient environment. In fact, salal shows a definite growth response to additions of macronutrients, particularly of nitrogen (Sabhasri 1961; UBC Bot. Garden 1970). It does not grow well in limy soils (UBC Bot. Garden 1970).

Water Relations: Salal will survive and grow under a variety of soil moisture conditions, but growth is most vigorous in moist conditions and the plant has poor vigour on shallow, droughty soils (Sabhasri 1961; Allen 1969; UBC Bot. Garden 1970; McMinn *et al.* 1976). In the Vancouver Forest Region, salal is found on soil moisture regimes ranging from very xeric to poorly drained (hygric), but tends to occur on the wetter soils in the driest subzones of the CDF, and is most abundant on the driest sites in wet subzones of the CWH (Klinka

[45] A. Banner, J. Pojar, and R. Trowbridge. 1983. Ecosystem classification of the Coastal Western Hemlock Zone, Queen Charlotte Island Subzone (CWHg), Prince Rupert Forest Region, British Columbia. B.C. Min. For., Smithers, B.C. Unpublished report.

[46] Yole *et al.*, 1982.

[47] A. Banner, J. Pojar, and R. Trowbridge. 1984. Representative wetland types of the Pacific Oceanic Wetland Region. B.C. Min. For., Smithers, B.C. Unpublished report.

1977*b*). Salal is abundant on very poorly drained bog woodlands in the CCPH[48] but in these ecosystems it tends to occur on elevated microsites.

Light Relations: Salal grows well in partial shade, but is uncommon and has very low vigour under dense forest canopies. Increasing light intensity by reducing overstory shade increases the vigour and growth rate of salal (Sabhasri 1961; Stanek *et al.* 1979; Koch 1983), but in most cases best growth is in light shade rather than in full sunlight (UBC Bot. Garden 1970; USDA 1974; Koch 1983). This may reflect evaporative stresses rather than an intolerance of sunlight (Koch 1983). Germination and survival of salal seedlings is not affected by low light intensities (Sabhasri 1961).

Although these field observations indicate that salal is at least a moderately shade-tolerant species, Sabhasri's (1961) laboratory research suggests that the photosynthetic and respiration characteristics of salal are similar to those of plant species classed as shade-intolerant. Growing plants are very sensitive to light conditions. There is a significant increase in photosynthetic activity and seedling growth with increased light intensities up to the maximum level tested (400 ft-candles). At low light intensities (100 ft-candles) respiration appears greater than photosynthesis. Maximum growth occurs under red light.

Temperature Relations: The geographic range of salal suggests that it may be sensitive to frost. This suggestion is supported by Sabhasri's (1961) observation that a short period of freezing temperature in the middle of May killed nearly all germinants.

GROWTH AND DEVELOPMENT

In nature, early growth of salal seedlings is very slow (M. Newton, pers. comm., Dec. 1984). Once established, the plant adds considerable quantities of biomass each growing season, but actual height increment is slower than for many other shrub species. Vigorous salal may grow to a height of over 2.5 m (Szczawinski 1962), but most plants average 60–120 cm in height (Clark 1976). The average new shoot increment during a growing season in western Washington was approximately 5 cm (Sabhasri 1961).

Leaves of salal normally live for 2–4 years, and occasionally last as long as 6 years. Twigs survive for 16 years or more, but only bear leaves during the first few years (Koch 1983). Individual plants survive for an indefinite period of time because of continued resprouting.

The root system of salal is shallow and very extensive. Plants expand outwards by means of rhizome-like root structures. Shoots consisting entirely of new growth were found up to 2 m from the parent plant (Koch 1983).

The total weight of new leaves added to a site in western Washington during the growing season averaged 900 kg/ha, while the total weight of salal biomass was approximately 36 000 kg/ha. Total root biomass exceeded the weight of above-ground parts (Sabhasri 1961).

Phenology: Phenological development of salal is highly variable (Stewart 1974*a*). In Washington, vegetative buds burst in early April. Vegetative growth occurred most rapidly from late April onward, peaking in early June (Sabhasri 1961).

Flowering can occur any time between March and July (USDA 1974), but commonly occurs during May and June in Alaska (Viereck and Little 1972). Near Vancouver, flowering took place between 12 June and 4 July in 1971 (Pojar 1974), while in western Washington, fruit set began by the 3rd week of June (Sabhasri 1961). Fruits ripen between August and October and are available on the stem until December (USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Pollination of salal flowers is by insects, primarily bumblebees and flies (Pojar 1974). The fruit is a many-seeded capsule with a fleshy outer calyx that forms a pseudo-berry. Fruits have an average of 126 seeds each. Heavy crops of fruit are produced on a regular basis, but fruiting was not observed by Koch (1983) under canopies with greater than 30.3% closure. Dispersal of the seeds is by birds and mammals who feed on the sweet fruit (Sabhasri 1961; USDA 1974).

Seed Viability and Germination: The fruits of salal are persistent and seeds remaining on the plant are viable for considerable periods following ripening. In cold, dry storage, the seed will remain viable for several years, but viability diminishes more rapidly under most natural conditions. The seeds do not appear to

[48] A. Banner, J. Pojar and R. Trowbridge. 1984. Representative wetland types of the Pacific Oceanic Wetland Region. B.C. Min. For., Smithers, B.C. Unpublished report.

require chilling to induce germination. A germination rate of 27–35% has been obtained from fresh seed under lighted conditions (Sabhasri 1961; USDA 1974).

Even though large quantities of seed are produced and numerous germinants may appear, very few seedlings survive in nature due to limitations of dispersal, seedbed conditions, and sensitivity to environmental extremes. Best germination was observed on decaying wood but survival and seedling development on this seedbed was poor. Seedling production is insignificant as a means of reproduction on most sites where salal is already established (Sabhasri 1961; Stewart 1978; Koch 1983).

Vegetative Reproduction: Once salal is present on a site, further expansion is almost exclusively by vegetative means (Sabhasri 1961; Koch 1983). Methods of vegetative reproduction include layering, and sprouting or suckering from roots and stem bases. Cuttings made from roots or stems readily form new roots and sprouts (Sabhasri 1961; Pojar 1974; Stewart 1974*b*; USDA 1974).

PREDATION AND PESTS

Fruits of salal are commonly eaten by grouse and other birds (Viereck and Little 1972). Mammals eating the fruit include black bear, black-tailed deer, and red squirrel (USDA 1974). The foliage is heavily browsed by black-tailed deer on the Queen Charlotte Islands.[49]

Of the numerous diseases known to occur on salal, the most common and serious is the leaf spot fungus (*Mycosphaerella gaultheriae*). The grey weevil also causes severe leaf damage to salal in southern B.C. (UBC Bot. Garden 1970).

EFFECTS ON CROP TREES

Competition: Salal is a common and serious competitor with coniferous tree species in low-elevation coastal B.C. Over most of its range, it is a competitor primarily on mesic and drier ecosystems, but it may occasionally become abundant on moister and richer ecosystems as well. Salal is capable of gaining nearly complete occupancy of a site and unlike most other brush species, is relatively insensitive to nutrient or water levels (Sabhasri 1961). Root competition, caused by the extensive, shallow root system, appears to be more significant than above-ground interactions such as shading or physical damage to seedlings. Salal is believed to provide serious competition for moisture on dry sites (Sabhasri 1961; Stanek *et al.* 1979), and recent investigations suggest that it can have a major impact on the nutrient budget of conifers (G. Weetman, pers. comm., Nov. 1984). Large quantities of nutrients can be tied up in salal biomass. A western Washington study (del Moral and Cates 1971) found no evidence of allelopathic chemicals in extracts of salal foliage and litter.

Competition is most severe during the early stages of stand development (Long 1977) but may continue throughout the rotation, particularly if the canopy is open enough to allow a well-developed understory of salal to persist (Stanek *et al.* 1979).

Beneficial Effects: Sabhasri (1961) could not demonstrate any negative impact of salal on Douglas-fir growth in his test plots in western Washington. In fact, control plots had significantly better growth than those plots where salal was manually removed. He noted that salal roots could make an important contribution to the organic matter content of the soil, and speculated that the loss of organic matter and associated nutrients caused by removal of the salal may have contributed to the poor growth of the seedlings.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Several studies indicate that salal biomass is inversely related to overstory cover, and salal will increase in cover, vigour, and height when the overstory cover is either reduced or totally removed (Sabhasri 1961; Long and Turner 1975; Long 1977; Stanek *et al.* 1979; Koch 1983). However, it apparently does not grow as rapidly as many other shrub species, and may take many years to become dominant following clearcutting.

Fire: Morris (1970) reported no major difference in salal cover on burned and unburned sites in Washington and Oregon. Fire is known to stimulate resprouting from roots and stem bases (Sabhasri 1961), but on slashburned areas, salal is generally slow to recover to preburn levels (G. Dunsworth, pers. comm., Dec.

[49] J. Pojar, T. Lewis, H. Roemer, and D.J. Wilford. 1981. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands. B.C. Min. For., Smithers, B.C. Unpublished report.

1984; B.M. Geisler, pers. comm., Jan. 1985). Severe burns on sites with dry, shallow soils can reduce salal cover if the fire penetrates sufficiently deep to kill the roots.

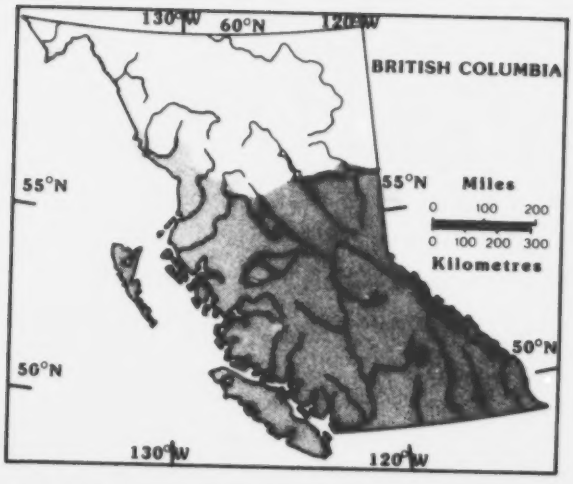
Cutting: Manual or mechanical cutting of salal can be expected to stimulate sprouting; the response may be similar to that following burning.

Herbicides: Conard and Emmingham (1984a) report that both glyphosate and 2,4-D cause only light (less than 25%) damage to salal. Triclopyr is somewhat more successful in controlling the species.

Soil Disturbance: Any form of soil disturbance that causes mechanical damage to salal but does not physically remove it from the site can be expected to stimulate resprouting. Pieces of stems and roots that are detached from the parent plant and buried in soil will root and form new plants (Sabhrasi 1961).

Fertilization: Salal responds to applications of fertilizer, particularly nitrogen, with increased above- and below-ground growth and vigour (Sabhrasi 1961; UBC Bot. Garden 1970). In forest stands, however, applications of fertilizer that result in an increase in the density of the tree canopy may cause a decline in vigour and cover of the salal understory (Long and Turner 1975; Stanek *et al.* 1979).

Lonicera involucrata (black twinberry).



Distribution of *L. involucrata* in British Columbia.

Lonicera involucrata (Richards.) Banks — Black twinberry (twinberry, honeysuckle)

DESCRIPTION:

Black twinberry is a straggling to ascending deciduous shrub 1–3 m tall. Stems have opposite branching and are four-sided when young. The leaves are elliptic to oblong, and untoothed. The yellow, tubular flowers occur in pairs above conspicuous green or purple bracts. The "twin" fruits are black to reddish round berries with few seeds (Viereck and Little 1972; Hultén 1974).

Variation: There are several forms of *L. involucrata*. The form occurring in British Columbia is the typical var. *involucrata* (UBC Bot. Garden 1979).

DISTRIBUTION AND ABUNDANCE

Black twinberry occurs throughout B.C. to approximately 57°N latitude. It is common on the Coast and in the Interior, and is found in all forested biogeoclimatic zones, but is absent from northern subzones of the BWBS. Black twinberry is present in the Peace River valley and is scattered in specialized habitats in the Stikine-Iskut drainage, but is apparently absent from the Fort Nelson and Liard River areas in the extreme north of B.C. (A. Češka, pers. comm., Nov. 1984). It is present but scattered throughout the outer coastal lowlands of the CCPH zone (J. Pojar, pers. comm., Oct. 1984) and is common in lowland areas of the Queen Charlotte Islands (UBC Bot. Garden 1979).

Altitudinal Range: Black twinberry is present from sea level to at least 1525 m in B.C. (UBC Bot. Garden 1979).

HABITAT

Climatic Relations: The range of black twinberry suggests that it tolerates quite a wide range of climatic extremes, but is not adapted to the extremely short growing season and harsh winter temperatures found in northern B.C. and at high elevations. In various parts of its range, however, black twinberry appears to be prevalent in frost pockets or areas of cold air drainage (R. Coupé and A. Češka, pers. comm., Nov. 1984).

Site and Soil Conditions: Black twinberry is a species of swamps, riparian habitats, alluvial soils, and moist woods (Lyons 1952; Viereck and Little 1972; Marchant and Sherlock 1984).

Nutrient Relations: Clark (1976) observes that black twinberry favours rich soil. Ecosystem associations in which black twinberry appears as a characteristic understory species are typically described as having a medium (mesotrophic) to very rich (eutrophic) nutrient status (Comeau *et al.* 1982; Pojar *et al.* 1982; Delong *et al.*[50]).

Water Relations: Black twinberry is described as being a species of moist or wet soils (Lyons 1952; Viereck and Little 1972; Marchant and Sherlock 1984). In areas of humid climate such as the Interior Wet Belt, it can be found on sites ranging from submesic to subhydric in moisture status; whereas in areas of drier climate it tends to be restricted to hygric and subhydric sites where some moisture in excess of precipitation is available through seepage or a high water table (Comeau *et al.* 1982; Angove and Bancroft 1983; Delong *et al.*[51]).

Light Relations: Black twinberry will tolerate semi-shade (Marchant and Sherlock 1984) but is most vigorous in open situations where sufficient moisture is available.

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

Phenology: Black twinberry breaks bud in April in the Kimsquit valley on the central B.C. coast (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.), and between early and late May on the east slope of the U.S. Rocky Mountains (Schmidt and Lotan 1980). In the Rockies, leaves are fully grown by mid-June, and leaf-fall occurs between late August and late September. In contrast, at Kimsquit, some leaves were fully expanded by mid-April. In early August, the first leaves began to turn yellow and most shrubs retained some leaves until October.

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[50] Delong *et al.*, 1984.
[51] Ibid.

Flowering begins after the leaves open from late May to early July in the Rocky Mountains (Schmidt and Lotan 1980). On the B.C. coast, flowering can begin in April (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.), and can extend from April to the end of August on some plants which continue to flower even as the fruits ripen (Clark 1976). Fruits ripen from mid-July to late August at low elevations in coastal B.C. (Marchant and Sherlock 1984; T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.); and throughout July only in the eastern Rockies (Schmidt and Lotan 1980).

REPRODUCTION

Seed Production and Dispersal: The glossy purplish black fruit of this species occurs in coalescent pairs. Each fruit has four to five seeds. Dispersal is primarily by birds and mammals (USDA 1974; UBC Bot. Gardens 1979); Cedar Waxwings are especially fond of the berries (Marchant and Sherlock 1984).

Seed Viability and Germination: Air-dried seeds can be stored for up to 15 years at 1–3°C without loss of viability, and for several years at least, at warmer temperatures (USDA 1974; Marchant and Sherlock 1984). The lengthy period of viability raises the possibility that black twinberry is a seed banker, whose seeds remain buried in the forest floor until conditions become conducive to germination. The seeds have some embryo dormancy and require a chilling period of 45–60 days for satisfactory germination to occur. A scarification treatment of the seed coat also improves germination. High germination percentages (56–80%) have been obtained under artificial conditions (USDA 1974; Marchant and Sherlock 1984).

Vegetative Reproduction: There are no reports of vegetative reproduction occurring in nature in this species. Several species of the genus sucker from a spreading root system (Jackson 1974), but there is no indication that this occurs in *L. involucrata*. Artificial cuttings taken during the dormant season rooted well when a rooting hormone was applied (Marchant and Sherlock 1984).

PREDATION AND PESTS

Black twinberry fruit are eaten by birds, bears, and other mammals (USDA 1974; UBC Bot. Garden 1979; Marchant and Sherlock 1984). Stems are browsed by moose, but it is not a preferred species. Marchant and Sherlock (1984) report that young plants are susceptible to leaf miner and that a leaf-deforming fungus that slows growth is prevalent in the southern Interior. The following diseases have been identified on *L. involucrata* in the wild in B.C.: *Kabatia lonicerae* var. *involucrata* (leaf spot), *Microsphaera penicillata* (powdery mildew), *M. alni*, *Leptophaeria dumetorum*, and *Ophiobolus minor* (UBC Bot. Garden 1979).

EFFECTS ON CROP TREES

Black twinberry is a competitor of moderate, but not major, importance throughout most of its range in B.C. It is primarily found as a component of a complex, vigorous brush community on moist productive ecosystems in many biogeoclimatic zones (C. Delong, R. Coupé, and D. Lloyd, pers. comm., Nov. 1984; J. Pollack, pers. comm., Jan. 1985). Very little is known about its competitive ability or any negative or beneficial effects that it may have on coniferous tree growth.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Eis' study (1981) in the SBS zone north of Prince George, showed that *L. involucrata* was present and numerous on both the Devil's Club and Alluvium site types prior to logging. Six years after the site was logged, black twinberry had become common on the *Aralia – Dryopteris* site type, had increased to greater than 25% cover on the Devil's Club site type, and had become the dominant species with 40% cover on the Alluvium site type. On the Alluvium site twinberry had produced a small quantity of seed and had almost reached a "mature" height by the end of the first season following logging. Shrub density increased for several years following logging and average height was 120 cm within 2.5 years. It took the shrubs 7 years to reach this same height on the Devil's club site type.

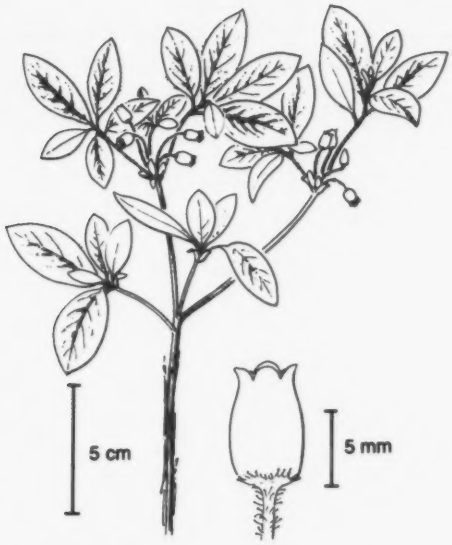
Fire: No information.

Cutting: No information.

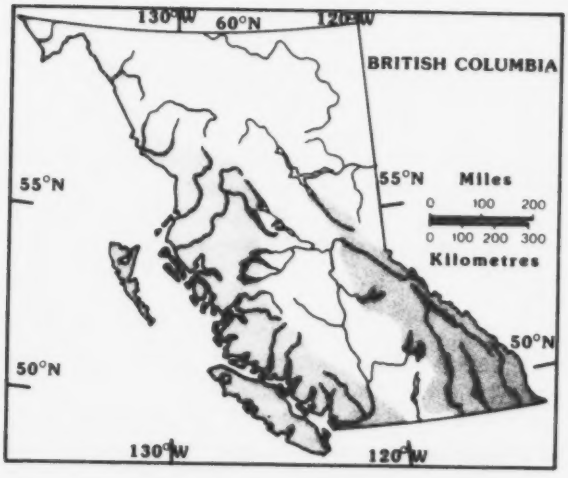
Herbicides: Glyphosate applied aerially as a midsummer spray at 2.25 kg/ha near Prince George, provided excellent (95%) 1st-year control of black twinberry. Total vegetative cover increased annually during the 2nd and 3rd years following treatment, but black twinberry itself did not recover (Expert Committee on Weeds

1984). In the Prince Rupert Forest Region, a foliar spray of 1.5 kg/ha glyphosate resulted in total top-kill, but response of the species in the 2nd year following treatment is unknown (J. Pollack, pers. comm., Jan. 1985).

Soil Disturbance: No information.



Menziesia ferruginea (false azalea).



Distribution of *M. ferruginea* in British Columbia.

Menziesia ferruginea Sm.

False azalea
(rusty menziesia, Pacific menziesia)

DESCRIPTION

False azalea is an erect, spreading, deciduous shrub to 2 m tall with slender, widely forking, opposite branches. Leaves are thin, oblong to obovate, finely hairy, and appear to be arranged in whorls. The leaves sometimes have a distinct bluish coloration. The small, yellowish red, bell-shaped flowers are borne in small clusters on shoots of the previous year. The fruit is a reddish brown ovoid capsule that splits along four partitions at maturity. The opened dry capsules often persist throughout the winter (Szczawinski 1962; Viereck and Little 1972).

Variation: Two subspecies of false azalea are found in British Columbia. *Menziesia ferruginea* ssp. *ferruginea* is found along the Coast and in the central Interior, while ssp. *glabella* is found in southeastern B.C. only. The latter subspecies is differentiated from the former by its more rounded leaves and greater pubescence (Szczawinski 1962; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

False azalea occupies coastal and mountain areas throughout the moist regions of B.C. It extends along the entire length of the province on the west side of the Coast Mountains and is also present in the Interior Wet Belt but is absent from the Interior Plateau and from all of northern B.C. east of the Skeena Mountains (Szczawinski 1962; Hickman and Johnson 1969). False azalea is present in all biogeoclimatic zones except the IDF, PPBG, BWBS, and SWB, but it is abundant only in the CWH, MH, ESSF, and CCPH zones.

Altitudinal Range: Along the Coast, false azalea is common from sea level to the alpine tundra, although it is generally absent in the CDF and drier CWH zones of the south Coast. East of the Coast Mountains, it tends to be found only at higher elevations, above approximately 900 m in the ICH and ESSF zones.

HABITAT

Climatic Relations: False azalea appears to require a fairly humid environment where only minor climatic moisture stresses are experienced during the growing season. This would explain why it occurs to sea level along most of the Coast, but retreats to more moist mountainous areas inland and along the Georgia Strait. The dry central Interior of B.C. is described as "climatically unsuitable" for *M. ferruginea* by Hickman and Johnson (1969). False azalea is also apparently unable to tolerate the extremely cold boreal climate of northeastern B.C. Hickman and Johnson (1969) report that throughout western North America it becomes dominant in areas of high rainfall or persistent fog or mist.

Site and Soil Conditions: Although primarily a species of mesic habits, false azalea can also occur on shallow rocky soils and in bogs (Hickman and Johnson 1969; Banner *et al.*[52]). Soils in areas where false azalea is a common component of the understory are predominantly Humo-Ferric or Ferro-Humic Podzols with a Mor humus (see e.g., Pojar (editor) 1983; Haeussler *et al.* 1984).

Nutrient Relations: In the cedar-hemlock forests of northern Idaho, false azalea is associated with soils low in potassium, and with a high organic matter content (Mueggler 1965). Ecosystem associations in which false azalea is a significant understory component are often classified as having very poor (oligotrophic) to medium (mesotrophic) nutrient status (see e.g., Klinka 1977*b*; Banner *et al.*[53]), but it can occur over a wide range of nutrient regimes.[54]

Water Relations: In areas of moist climate, false azalea is most abundant on well- to moderately well-drained soils with a more-or-less mesic moisture status (Hickman and Johnson 1969; Viereck and Little 1972; Klinka 1977*b*). In very wet climates, both in the Interior and on the outer Coast, false azalea can be very abundant on some of the most rapidly drained xeric sites (Angove and Bancroft 1983; Banner *et al.*[55]; Delong *et al.*[56]). The species is also abundant in poorly drained coastal bogs (Hickman and Johnson 1969; Banner *et al.*[57]).

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[52] Banner *et al.*, 1984.
[53] Banner *et al.*, 1983.
[54] Utzig *et al.*, 1983.
[55] Banner *et al.*, 1983.
[56] Delong *et al.*, 1984.
[57] Banner *et al.*, 1984.

Light Relations: False azalea is a common species of deeply shaded climax, western hemlock forests (Szczawinski 1962; Viereck and Little 1972). Its ability to persist in these heavily shaded forest understories in which light intensities are typically 5% of full light (P. Alaback, pers. comm., Dec. 1984), indicates that it is very shade-tolerant. The species usually displays better vigour in the partially shaded conditions of forest openings than under a closed forest canopy.

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

False azalea can reach heights of 3 m at maturity (Viereck and Little 1972), but it is usually no more than 2 m tall (Clark 1976).

Phenology: In Alaska, false azalea flowers from late May through July. The capsules mature in July and August (Viereck and Little 1972).

REPRODUCTION

No information is available regarding the biology of seed production, dissemination and seedling germination. The dry capsule of false azalea contains numerous tiny seeds and opens through natural dehiscence (Szczawinski 1962), which probably means that seed is dispersed by gravity and wind, rather than by animal vectors.

Vegetative Reproduction: Miller (1977) indicates that *Menziesia* is a root-crown sprouting species and does not spread by means of rhizomes.

EFFECTS ON CROP TREES

False azalea is a common component of a complex of Ericaceous tall shrubs (including *Vaccinium* spp. and *Rhododendron albiflorum*) that is abundant on well-drained, usually more-or-less mesic sites along the coast of B.C. and in moist mountainous areas of the Interior. Although this complex of shrubs is very abundant and often dominates on clearcut sites, virtually nothing is known about its effect on the regeneration and growth of crop trees. In coastal B.C., the *Vaccinium – Menziesia* shrub community is rarely a specific target of vegetation management efforts, because it is not perceived as having a significant detrimental impact on the regeneration of conifers. In contrast, in some areas of the southern Interior, such as the ESSF zone in the Kamloops region, the *Rhododendron – Vaccinium – Menziesia* complex is believed to be a major brush problem (W.R. Mitchell and D. Lloyd, pers. comm., Nov. 1984; M. Tanner, pers. comm., Jan. 1985). False azalea is rarely the most abundant or aggressive species in this complex.

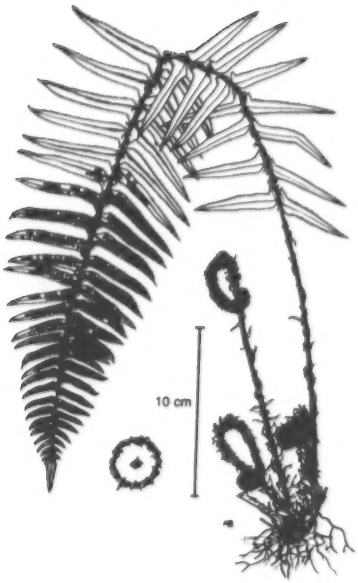
RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: In the cedar-hemlock forests of northern Idaho, there was no significant difference between the cover and frequency of false azalea on logged and unlogged sites (Mueggler 1965). Biomass of false azalea in early successional stands (up to 30 years) in southeastern Alaska was 3 times greater than the biomass in climax western hemlock – Sitka spruce forest (Alaback 1981).

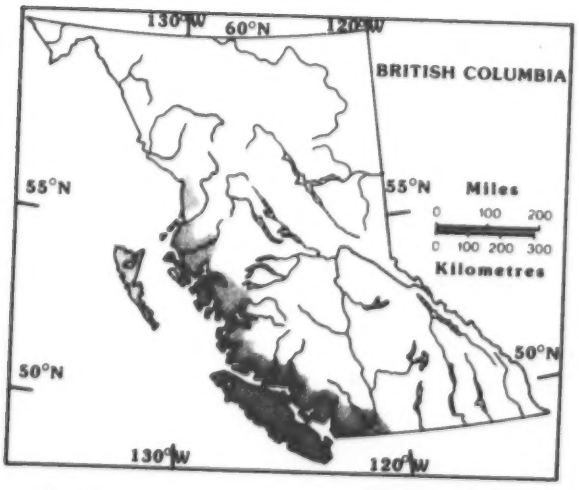
Fire: False azalea is a fire-sensitive species (Stickney 1981). Miller (1977) speculates that it will sprout from the root crown after a burn, but will not produce suckers. Fire appears to have totally removed this species from experimental plots in Washington and Oregon, for up to 16 years (Morris 1970). In western Montana, Stickney (1981) found that survival of false azalea was low and it was very slow to redevelop after fire, especially on areas that had been intensely burned. However, Mueggler (1965) reported no significant difference in cover and frequency between burned and unburned areas in northern Idaho.

Herbicides: When glyphosate was applied to false azalea by Micron Herbi as a foliar spray at 500 g a.i./ha in the Kamloops Forest Region, many stems were at least partially killed, and 2 years later the foliage of surviving stems remained dwarfed and deformed.[58]

[58] Whitehead *et al.*, 1982.



Polystichum munitum (sword fern).



Distribution of *P. munitum* in British Columbia.

Polystichum munitum (Kaulf.) Presl. — Sword fern

DESCRIPTION

Sword fern is a large fern with stiff, erect fronds up to 1.8 m tall, rising from a stout, woody rhizome. The blades are evergreen, linear to lanceolate, with numerous toothed, sharp-pointed pinnae. The pinnae have a characteristic hilt-like projection near the base (Taylor 1973*a*; Wagner 1979).

Variation: Size and frond shape vary widely, particularly in response to environmental conditions (Taylor 1973*a*). A type of sword fern with a very narrow linear blade and closely crowded overlapping pinnae is common in exposed locations. There is some disagreement as to whether this fern represents an ecological form of *P. munitum* (forma *imbricans*) produced in response to extreme environmental conditions (Frye 1934; Taylor 1973*a*; Taylor and MacBryde 1977), or whether it is a distinct taxon (Wagner 1979).

DISTRIBUTION AND ABUNDANCE

Sword fern is widespread and common west of the Coast Mountains along the entire length of British Columbia, including the Queen Charlotte Islands. In the U.S., the species extends inland to northern Idaho and Montana, and northern outliers are found in moist forests of the west Kootenays (Wagner 1979). Sword fern is abundant in the CDF and CWH biogeoclimatic zones, locally common in the CCPH, uncommon in the MH zone, and rare in the ICH zone.

Altitudinal Range: Sword fern is primarily a low-elevation species in B.C. In southwestern B.C. it was rarely found at elevations above 900 m (Brooke *et al.* 1970). On the north Coast it is even more restricted in elevation, and is rarely found more than 100 m above sea level.

HABITAT

Climatic Relations: The geographic and altitudinal range of this species suggests that it requires a humid coastal climate with mild winters. It does occur in areas of moist, relatively mild continental climate in Idaho and Montana and adjacent areas of B.C., but in these areas it tends to favour the shaded, moist northern aspects (Mueggler 1965). The evergreen frond of sword fern may be a limiting factor in its ability to survive in areas with cold winters.

Site and Soil Conditions: Sword fern will grow on a wide variety of parent materials including exposed bedrock, but the most luxuriant growth is found on deep loamy soils, especially those developed on fluvial parent materials (see e.g., Klinka and Carter 1980).

Nutrient Relations: Sword fern grows best and is most abundant on fertile soils (Taylor 1973*a*; McMinn *et al.* 1976). Ecosystem associations with this species as a characteristic understory species are usually described as having a medium (mesotrophic) to very rich (eutrophic) ecological nutrient status (see e.g., Klinka 1977*a*; Yole *et al.*[59]). When abundant and vigorous, swordfern is often considered to be an indicator of nutrient-rich sites.

Water Relations: Sword fern is characteristically found in moist or shaded locations, where drainage is good, but little moisture stress is encountered. In the CDF zone of southern Vancouver Island, where summer moisture deficits are common, it is found only where seepage water augments the soil moisture supply (McMinn *et al.* 1976). In wetter climates it is less restricted by soil moisture supply. Ecosystem associations in which sword fern is abundant typically have a mesic to hygric moisture status (see e.g., Klinka 1977*a*).

Light Relations: Sword fern is apparently quite shade-tolerant since it typically occurs in the understories of mature forests and favours shady sites or north aspects (Mueggler 1965; Taylor 1973*a*). In clearcut areas it often prefers protected, shaded locations.[60] This probably reflects sensitivity to high evapotranspirative losses rather than intolerance of light itself. When plants of *P. munitum* are subjected to increased insolation through removal of overstory shade, the fronds become dwarfed and more erect and the pinnae become crisped (Frye 1934; Taylor 1973*a*; Wagner 1979).

Temperature Relations: The evergreen frond of sword fern is presumably at least moderately resistant to frost.

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[59] Yole *et al.*, 1982.
[60] Brand, 1984.

GROWTH AND DEVELOPMENT

See *Athyrium filix-femina* (page 51) for a simplified explanation of the fern life cycle. The growth and development of sword fern is probably quite similar to that of lady fern except that sword fern fronds are evergreen and thus persist for several years. At maturity the frond is 60–180 cm in length and approximately 25 cm wide (Taylor 1973*a*; Wagner 1979).

Phenology: Stewart (1976) reported that in Oregon, sword fern fronds were partially unfurled on 26 May 1970. By 28 July the fronds were mature and spores were nearing maturity.

REPRODUCTION

Spore Production and Dispersal: Most medium-sized forest ferns begin to produce spores at between 1 and 5 years of age and spore production takes place very regularly from year to year. The vigour of the plant, as influenced by its habitat, is an important determinant of plant fertility. Most ferns similar in size to *P. munitum* produce tens of millions of spores on each frond. The tiny spores are ejected into the air when mature and are carried away by gravity, wind, water, or animals. Evergreen ferns like *Polystichum* can retain some spores on the fronds over winter for dissemination the following spring. Fern spores are capable of travelling thousands of miles, but in forests there may be a lack of air currents to carry them aloft. Airborne spores are often brought to earth during rainstorms (Page 1979).

Spore Viability and Germination: Fern spores in a dry, resting state are quite resistant to physical extremes and can withstand intense radiation and very low temperatures. They are reportedly very sensitive to temperatures above 55°C (Kato 1963; Miller 1968). Under ideal conditions, fern spores remain viable for 2–4 years, but their viability and the speed of germination deteriorates with age (Page 1979). Spores usually germinate only after being soaked in water. Like most fern spores, the spores of sword fern germinate best when exposed to light, but sword fern is one of only a few fern species in which some germination will occur in darkness (Weinberg and Voeller 1969).

Vegetative Reproduction: Vegetative reproduction of sword fern can occur through division of its perennial, woody rhizome. The rhizome becomes somewhat branched with age (Wagner 1979), but is apparently not creeping, like that of *Pteridium aquilinum*. Although the species often occurs in pure, uniform stands, these stands probably represent populations of individual sporophytes rather than clones.

PREDATION AND PESTS

In Oregon, this species is known to be a major winter food of the mountain beaver (Stewart 1976), a species that has a very restricted range in southwestern B.C. (McTaggart-Cowan and Guiguiet 1965). Deer, elk, and black bear also forage on this fern (Frye 1934; Pojar *et al.*[61]).

EFFECTS ON CROP TREES

Competition: Sword fern is a dominant species of understory vegetation on some of the most productive growing sites for Douglas-fir and other conifers in B.C. (Wagner 1979; Klinka and Carter 1980). However, it is not considered a serious or major competitor on the Coast since it interferes significantly with the regeneration and growth of conifers only in localized areas where it is extremely abundant or vigorous (Stewart 1976; Brand;[62] M. Scott, pers. comm., Nov. 1984). Reduction or elimination of sword fern from conifer plantations may reduce competition for moisture and light and may reduce the desirability of these plantations as habitat for tree-damaging mammals (Stewart 1976), but the magnitude and exact nature of the competitive effect have not been studied. Del Moral and Cates (1971) studied the allelopathic potential of sword fern in western Washington, and found no evidence of inhibitory chemicals under either laboratory or field conditions.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Limited evidence suggests that sword fern initially decreases in cover following logging (M. Scott, pers. comm., Nov. 1984; B.M. Geisler, pers. comm., Jan. 1985), but that it slowly recovers

[61] Pojar *et al.*, 1981.

[62] Brand, 1984.

(Lafferty 1972). Following logging of moist, productive sites in the CWH zone near Vancouver, sword fern, previously an important understory species, could only be found in shady spots under a protective canopy of bigleaf maple.[63] It seems likely that sword fern, like lady fern, is able to maintain its cover on sites where soils remain moist after logging, and that its cover is diminished on exposed and drier sites where evapotranspirative stresses are severe. The fronds often become dwarfed in size following exposure to dry air and strong light (Frye 1934; Wagner 1979).

Fire: Slashburning studies in CWH zone near Vancouver show that sword fern is capable of surviving even an intense fire (Lafferty 1972), but on some sites it may be absent for the first few years following a fire or restricted to unburned patches only.[64] Morris (1970) found that sword fern was equally abundant on burned and unburned clearcut areas from the third to the 16th season following burning in western Washington and Oregon.

Cutting: No information.

Herbicides: Stewart (1976) tested four herbicides as early foliar (26 May) and midsummer (28 June) sprays on sword fern in Oregon. Dicamba and bromacil were effective in controlling sword fern at any time between mid-May and mid-July. In western Washington and Oregon, glyphosate causes very severe (greater than 90%) injury when applied in late summer and moderate (25–60%) injury when applied in the fall (Conard and Emmingham 1984*a*).

Soil Disturbance: No information.

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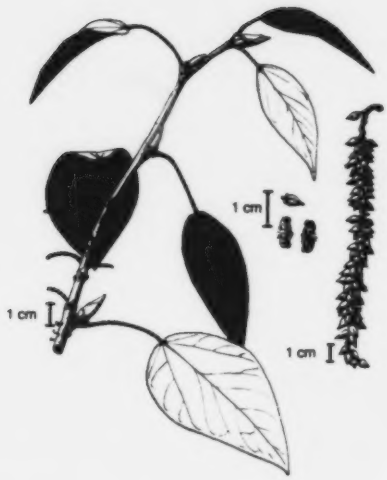
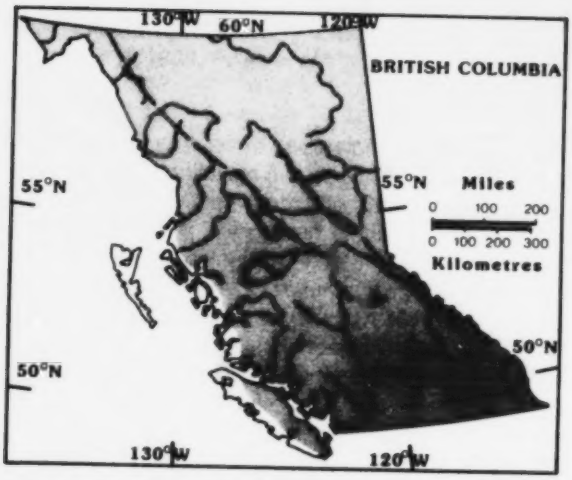
[63] Brand, 1984.
[64] Ibid.



Populus balsamifera ssp. *balsamifera* (balsam poplar).



Distribution of *P. balsamifera* in British Columbia. The dashed line indicates the approximate boundary between ssp. *balsamifera* (balsam poplar) to the north and east, and ssp. *trichocarpa* (black cottonwood) to the south and west. Specimens intermediate between the two subspecies are common where their ranges overlap.

Populus balsamifera L. ssp. *balsamifera* — Balsam poplar

DESCRIPTION

Balsam poplar is a deciduous tree with a long straight trunk and an open crown, reaching 35 m in height and 60–80 cm in diameter. The bark is grey and deeply furrowed. The twigs are stout with large, pointed, resinous buds. Leaves are broadly lanceolate to ovate and untoothed. The fluffy seeds are produced on long drooping catkins (Hosie 1973; Hultén 1974).

Variation: No geographic varieties of balsam poplar are described in British Columbia (Taylor and MacBryde 1977). Balsam poplar hybridizes extensively with the closely related black cottonwood *(P. balsamifera* ssp. *trichocarpa)*, and may hybridize with *P. tremuloides* in some areas (Hosie 1973; Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Balsam poplar is found across Canada but is replaced by black cottonwood through most of B.C. In this province, it is restricted to areas adjacent to or east of the Rocky Mountains in the Peace River and Fort Nelson lowlands (Hultén 1974) and east of the Rocky Mountain Trench (Krajina *et al.* 1982). It extends westward in northern B.C. to the Stikine Plateau. Balsam poplar is abundant in the BWBS zone, less common in the SWB zone, and occurs sporadically in some eastern subzones of the SBS, IDF, and ICH (Krajina *et al.* 1982).

Altitudinal Range: Balsam poplar grows from sea level in Alaska to 1650 m elevation in the Rocky Mountains (Fowells (compiler) 1965). It is primarily a lowland species (Hosie 1973; Zasada *et al.* 1981).

HABITAT

Climatic Relations: Balsam poplar is primarily a species of boreal climates, although it ranges from arctic to temperate climates. The boreal climate is characterized by frozen ground and snow cover for 6 or more months duration with the average temperatures below −3°C during the coldest month and rarely above 10°C in the warmest month (Krajina *et al.* 1982).

Site and Soil Conditions: Balsam poplar is most commonly found on moist upland and alluvial bottomland sites. It exhibits its best growth on moist, rich bottomlands with deep soil. Where balsam poplar occurs together with black cottonwood, the cottonwood generally inhabits the alluvial sites, and balsam poplar the uplands. Balsam poplar rarely grows on dry, exposed sites. Soils supporting balsam poplar vary widely and include gravels, deep sands, clay loams, silts, silt loams, and shallow organic soils, but not deep peats (Fowells (compiler) 1965; Hosie 1973; Brayshaw 1978; Zasada *et al.* 1981).

Nutrient Relations: The nutrient requirements of balsam poplar are high; it does not tolerate acid mor humus forms in which nutrients are slowly released. Balsam poplar requires a good supply of calcium and magnesium and prefers nitrates to ammonium as a supply of nitrogen (Krajina *et al.* 1982). In the BWBS zone of northeastern B.C., it is most abundant on river terraces described as having a rich nutrient status.

Water Relations: An abundant supply of soil moisture is critical for good growth of balsam poplar (Fowells (compiler) 1965), but it does not tolerate brackish water. It is most often found on sites with a subhygric to hygric moisture status. Flood resistance of balsam poplar is possibly the highest among the trees growing in B.C. (Krajina *et al.* 1982).

Light Relations: Balsam poplar has very low to nonexistent shade tolerance (Krajina *et al.* 1982). Best growth and development occur in full sunlight; it will not grow in competition with other species unless it is in a dominant position (Fowells (compiler) 1965).

Temperature Relations: The frost resistance of balsam poplar is very high; it can become established in areas of permafrost (Krajina *et al.* 1982). In the taiga of interior Alaska, balsam poplar grows on sites with low soil temperature, where surficial soil layers do not completely thaw until well into the growing season and frosts are common well into June (Foote 1983).

GROWTH AND DEVELOPMENT

Balsam poplar is characterized by rapid early growth that allows it to establish and maintain dominance above competing vegetation. Rapid growth can be maintained for the first 40–50 years of life by which time it can reach heights of 25 m and diameters of 45 cm. On good sites it will outgrow aspen. Mature trees in southern Alaska average 35 m in height and 66 cm in diameter (Foote 1983); however, trees in eastern North America are

typically smaller (Fowells (compiler) 1965; Hosie 1973). Balsam poplar is relatively short-lived in southern parts of its range but can live as long as 200 years in Alaska (Fowells (compiler) 1965; Foote 1983). It normally has a shallow root system (Hosie 1973), especially on wet soils or where permafrost is present at shallow depths.

Phenology: The catkins flower between April and June before the leaves appear. The seed matures very early, from mid-May to mid-June when the leaves are about two-thirds grown. Seed dispersal occurs immediately after the seeds are mature. Flowering and seed maturation times appear to be regular from year to year within ecotypic ranges (Fowells (compiler) 1965; USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Balsam poplar first flowers between 8 and 10 years of age (USDA 1974), and subsequently produces a good seed crop every year (Lutz 1955). The seeds have downy plumes, and are readily distributed by wind (Fowells (compiler) 1965; Brayshaw 1978), but seed deposition is greatly reduced at distances greater than 100–200 m from the seed source (Zasada *et al.* 1981).

Seed Viability and Germination: Balsam poplar seed remains viable for only a few days following dispersal (Fowells (compiler) 1965). It has no dormancy requirements and germinates immediately following arrival on a suitable seedbed (Lutz 1955). Thus most germinants appear in early summer. In an Alaska study, more than 80% of total germinants appeared within 2 weeks of artificial seeding; seedlings continued to appear for 3–4 weeks (Zasada *et al.* 1983).

Young balsam poplar seedlings are extremely susceptible to drying, rain damage, and soil fungi. They require at least one month of abundant moisture to ensure survival (USDA 1974). Zasada *et al.* (1981) observed no seedlings establishing on organic and gravel surfaces at an alluvial site in Alaska following harvesting of a balsam poplar overstory, but regeneration by seed is very common on these river bottom sites (Zasada 1971). Lutz (1955) reports abundant balsam poplar seedlings wherever mineral soil is exposed and a seed source is available.

Vegetative Reproduction: Balsam poplar will regenerate vegetatively from root suckers as well as from stump sprouts and buried branch pieces (Lutz 1955; Zasada *et al.* 1981). Stump sprouts originate from either dormant buds or from callus tissue. Callus sprouts usually originate at the top of a cut stump, or form where a stump has been damaged during logging. Most root suckers grow from roots of approximately 1 cm in diameter that occur within the top 2 cm of the soil. Suckers also develop from exposed roots. Suckering is significantly less in gravelly soil than in silty soils and is greatest where the organic layer has been removed, exposing mineral soil. Branch parts must be well buried in the soil to produce aerial shoots (Zasada *et al.* 1981). Sucker regeneration is probably more important than regeneration from seed for balsam poplar in Alaska (Lutz 1955).

PREDATION AND PESTS

Primary disease and insect pests of balsam poplar are discussed in Fowells (compiler, 1965).

EFFECTS ON CROP TREES

Competition: There are no quantitative data on the effect of balsam poplar competition on conifers. Its growth easily outstrips the growth rates of young conifers, especially when it is of sucker origin. White spruce is the primary crop species occurring in association with balsam poplar, and many of the most productive alluvial growing sites in the boreal forest are occupied by fairly pure seral stands of balsam poplar (Neiland and Viereck 1977; Foote 1983). White spruce almost always succeeds balsam poplar on floodplains, but there is a complete lack of coniferous regeneration in most of these stands (Foote 1983). Balsam poplar has been shown to have an allelopathic effect on the germination and early growth of green alder (Jobidon and Thibault 1981).

Beneficial Effects: There are no reports in the literature of beneficial effects of balsam poplar on the growth of coniferous trees. It plays an important role in stabilizing river banks and maintaining river islands, and may be a valuable crop tree in northern B.C.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Trees cut or damaged during logging will sprout from the stump or sucker from the roots; seedling germination will likely occur on areas of exposed mineral soil if a seed source is available (Lutz 1955; Zasada *et al.* 1981).

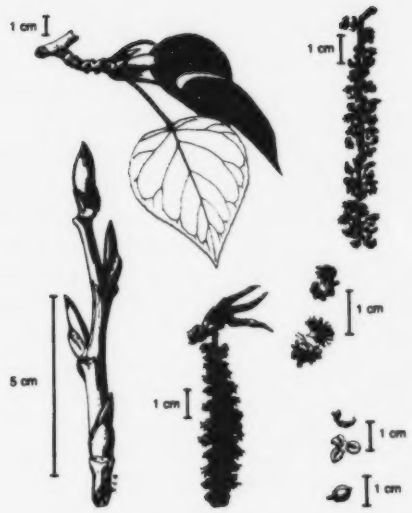
Fire: Of the tree species of the northern boreal forest, balsam poplar is perhaps the most resistant to destruction by fire (Lutz 1955). Like aspen, balsam poplar is stimulated to produce root suckers following fire. In Alberta, the majority of balsam poplar suckering occurred during the second season following spring burning of a 15-year-old stand (Bailey and Anderson 1979). Density after 5 years was greater on burned areas than on unburned areas.

Cutting: In an Alaskan study (Zasada *et al.* 1981), more than 50% of mature balsam poplar cut during the summer, fall, and winter produced sprouts from callus tissue and dormant buds. Many stumps had more than 25 sprouts after the first growing season. Sprout survival on trees cut in the fall and winter was good, but less than 15% of the trees cut in the summer had surviving sprouts after 4 years. Stump sprouting was most pronounced on winter-logged areas, and sprouts originating from dormant buds were most common after winter logging. Cutting also stimulates suckering from the roots, but there are no studies documenting suckering response.

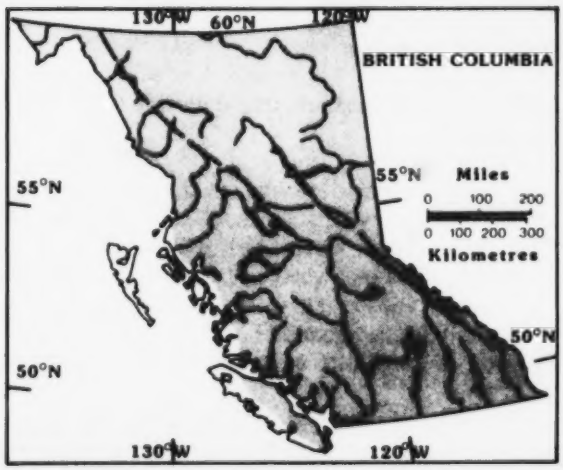
Herbicides: Balsam poplar was less sensitive than aspen when sprayed with 2,4-D in the dormant season (Bowes 1981). Rates of 2.2 kg/ha had virtually no effect and a rate of 4.4 kg/ha provided only marginal control. In separate greenhouse studies, balsam poplar was not killed by 2,4-D at rates up to 2000 ppm (Corns and Dai 1967). In Alberta, mortality was high on 1st-year suckers sprayed with 2.2 kg/ha of 2,4-D as a midsummer foliage spray, but spraying did not prevent further suckering from taking place the following year (Bailey and Anderson 1979).

Glyphosate appplied by either backpack spray or aerially at 2.4–3.0 kg/ha has provided good to excellent control of balsam poplar. The majority of stems were completely killed with little subsequent suckering. Hexazinone applied as a liquid spray, by soil injection, or in granular applications also provided good control of balsam poplar; however, results were variable, especially on areas with deep organic layers (Expert Committee on Weeds 1984).

Soil Disturbance: Exposure of mineral soil favours germination of balsam poplar seed and may promote root suckering by increasing soil temperatures. Branch fragments buried as a result of soil disturbance have a high likelihood of regenerating (Lutz 1955; Zasada *et al.* 1981). Following heavy flooding, balsam poplar quickly sends out new roots into the freshly deposited silt layers (Neiland and Viereck 1977).



Populus balsamifera ssp. *trichocarpa* (black cottonwood).



Distribution of *P. balsamifera* in British Columbia. The dashed line indicates the approximate boundary between ssp. *balsamifera* (balsam poplar) to the north and east, and ssp. *trichocarpa* (black cottonwood) to the south and west. Specimens intermediate between the two subspecies are common where their ranges overlap.

oulus balsamifera L. ssp. *trichocarpa* (Torr. & Gray) Braysh. **Black cottonwood**
trichocarpa)

SCRIPTION

Black cottonwood is a tall, deciduous tree, up to 40 m tall and 150 cm in diameter. The grey bark of mature s is deeply furrowed; young bark is smooth. Twigs are stout and hairless, with large, resinous, pointed buds. arate male and female flowers form long, drooping catkins which split to release seeds bearing cottony n. Black cottonwood differs from balsam poplar in having wider leaves and a three-valved rather than a two- ed fruit (Hosie 1973; Brayshaw 1978).

ation: There are many intermediate forms between this subspecies and ssp. *balsamifera* where the ranges of the two overlap in northern British Columbia (Brayshaw 1978).

TRIBUTION AND ABUNDANCE

Black cottonwood is found throughout southern and central B.C. to the edge of the Rocky Mountains. It is ent along the outer Coast including northern Vancouver Island and the Queen Charlotte Islands. In northern ., it is present adjacent to the Alaska Panhandle but is replaced by balsam poplar inland (Brayshaw 1978; ina *et al.* 1982). It is found in all biogeoclimatic zones except the CCPH, SWB, and AT, and is most abundant ajor river valleys throughout the province.

udinal Range: Although primarily a species of valley bottoms, black cottonwood ranges from sea level to the lower limits of the MH zone on the B.C. Coast (Packee 1976), and has been recorded as high as 2100 m elevation in the Selkirk Mountains of the Interior (Fowells (compiler) 1965).

BITAT

natic Relations: Black cottonwood grows in climates ranging from relatively arid to humid, but achieves its best development in areas of humid climate (Fowells (compiler) 1965). It is absent from the cool, perhumid areas of the outer B.C. coast, and is replaced by balsam poplar in the severe boreal climate of northeastern B.C. (Brayshaw 1978). It occurs marginally in subalpine climates (Krajina *et al.* 1982).

and Soil Conditions: Black cottonwood is characteristically associated with river banks, gravel bars, or low- lying land, but it also grows on the loams, clays, and rich humic soils of upland sites. Typical soils are young with little soil development. The largest trees grow at low elevations on deep alluvial soils, while the poorest growth is on newly deposited gravel (Lyons 1952; Roe 1958; Fowells (compiler) 1965).

rient Relations: Nutritional requirements of black cottonwood are high. Like balsam poplar it requires a good supply of calcium and magnesium and does not grow well on acid mor humus forms where nutrients are released slowly (Krajina *et al.* 1982). A pH of 6–7 is required for optimum growth (Smith 1957, cited by Packee 1976). Black cottonwood commonly grows on deep alluvial soils that are among the richest, most productive growing sites in B.C.

er Relations: Black cottonwood requires abundant, well-oxygenated water for optimum growth (Smith 1957, cited by Packee 1976). It is highly tolerant of flooding, and grows abundantly on sites that receive regular flooding, but it does not tolerate the brackish water that forms near the ocean or in stagnant pools following flooding. Fine sediment deposited by flooding tends to reduce soil aeration and inhibits cotton- wood growth, whereas fast-moving water, rich in oxygen speeds growth (Fowells (compiler) 1965; Krajina *et al.* 1982). Black cottonwood apparently has low tolerance of drought, and throughout most of its range is restricted to sites receiving supplemental moisture. In areas of dry climate it survives in protected valleys and canyon bottoms where the roots can reach a permanent supply of soil moisture (Fowells (compiler) 1965).

t Relations: Black cottonwood is a shade-intolerant species (Fowells (compiler) 1965; Krajina *et al.* 1982) that grows best in full sunlight. It does not survive in a forest understory.

perature Relations: While dormant, black cottonwood is one of the most frost-resistant trees in the northwestern U.S. (Minore 1979); however, it can be killed or damaged by late fall frosts (Fowells (compiler) 1965). It is presumably less tolerant of cold temperatures than balsam poplar (Krajina *et al.* 1982).

OWTH AND DEVELOPMENT

Black cottonwood exhibits rapid juvenile growth that outstrips that of its competitors, allowing it to establish maintain a dominant position in a stand (Packee 1976). Exceptional trees can reach 13.7 m in height and 18

cm diameter in 7 years; by age 27 black cottonwood can exceed 36 m in height and 80 cm in diameter. It is the largest growing deciduous tree in B.C. Maturity is normally reached in 60–70 years, but good growth can be maintained for as long as 200 years. Best growth occurs on coastal sites, with growth decreasing towards the north and in interior locations (Fowells (compiler) 1965; Hosie 1973).

The tree develops a long straight bole and is normally free of branches for most of its length. Young trees have a narrow, conical crown with upswept branches (Lyons 1952). The root system is shallow and wide-spreading (Hosie 1973).

In cutover areas, large numbers of sprouts are produced from cut stumps. With the possible exception of red alder, vigorous cottonwood sprouts are the fastest growing plants on recently logged coastal alluvial sites on the Skeena River (J. Pollack, pers. comm., Jan. 1985).

Phenology: The flowers of black cottonwood appear from late March or early April through to late May on the Coast, and can appear as late as mid-June in some areas of the Interior. Leaf emergence follows flowering. Fruits are ripe within a month of flowering, and seed dispersal is as early as late May to early July. Trees of northern and inland provenances cease growth earlier in the growing season than provenances from south coastal areas (Fowells (compiler) 1965).

REPRODUCTION

Seed Production and Dispersal: Black cottonwood becomes sexually mature at approximately 10 years of age. Good seed crops are produced annually. The downy seed is light and buoyant and can be transported for long distances by wind and water (Fowells (compiler) 1965; USDA 1974).

Seed Viability and Germination: The viability of fresh seed is high, but of short duration (Fowells (compiler) 1965). Cottonwood seed will readily germinate on a variety of favourable sites (Beals 1966), particularly where bare soil has been exposed or new soil laid down. Moist seedbeds are essential for high germination rates and seedling survival depends on favourably moist conditions for at least the 1st month (Roe 1958; USDA 1974). Seedling establishment is the primary means of reproduction of black cottonwood in the Cariboo Forest Region[65] and probably throughout B.C.

Vegetative Reproduction: Sprouting from the stump is the most common form of vegetative reproduction in black cottonwood, although minor root suckering also occurs (Roe 1958). Sprouts arise primarily from suppressed buds on the stump, but can also originate in wound callus (Debell and Alford 1972). Black cottonwood is also known to regenerate from broken stem or root fragments incorporated in moist mineral soil. An unusual form of vegetative reproduction has been reported by Galloway and Worrall (1979). Small shoots, complete with green leaves, abscise naturally and either root where they fall, or are transported some distance by water before taking root.

Artificial regeneration can be successfully achieved using stem cuttings. For best results the cuttings should be collected from mid-December to mid-February from young saplings 2–3 m tall. Cuttings should average 1–2 cm in diameter and 35–45 cm in length. Early spring planting is recommended. Survival of unrooted cuttings is as good as, or better than, survival of artificially rooted cuttings (Stine *et al.* 1981).

PREDATION AND PESTS

Principal disease and insect pests are described by Fowells (compiler, 1965). Damage to young trees from small mammals, especially voles or meadow mice, can be severe on grassy or herb-covered sites. Rabbits and hares can girdle the base of young trees and cause clipping damage (D. Debell, pers. comm., Dec. 1984). Black cottonwood is a source of browse for ungulates, and is heavily used by beaver.

EFFECTS ON CROP TREES

Competition: Black cottonwood is a severe competitor with conifers because of its rapid height growth and early dominance of forested sites. Competition is most severe on extremely productive bottomland sites, and will continue for the length of the rotation. Early competition comes from plants of both sprout and seed origin. Cottonwood plants may be extremely dense in the first few years of growth, but self-thinning will normally take place by age 5 as weaker trees are quickly suppressed by the more dominant plants (Roe 1958).

[65] Perry, 1983.

Beneficial Effects: There are no reports in the literature of beneficial effects of cottonwood on the growth of coniferous trees. It plays a very important role in stabilizing river banks and maintaining river islands, and can be a valuable short-rotation crop tree in its own right.

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Black cottonwood is not found as an understory species beneath mature forest canopies. Following logging, seeding-in will occur from residual or nearby trees. Trees cut during logging will sprout profusely and may produce some root suckers (Roe 1958).

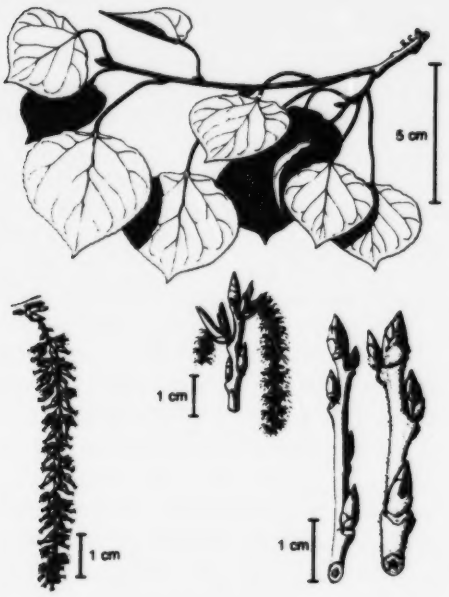
Fire: Black cottonwood is highly susceptible to fire and even light burns can cause considerable injury (Fowells (compiler) 1965). Cottonwood is apparently not a fire-adapted species, but there are no reports in the literature documenting its response to natural or prescribed fire.

Cutting: Young black cottonwood respond to cutting with vigourous sprouting. Repeated cutting on a 2-year cycle does not significantly affect sprouting vigour (Debell *et al.* 1984). Debell and Alford (1972) found that when 2-year-old trees were cut in February to a 30-cm stump, sprouts were abundant after two growing seasons. Most sprouts arose from dormant buds more than 15 cm above the ground level. When the same trees were cut to 15 cm in height 2 years later, they sprouted more slowly and some sprouts arose out of callus tissue. These adventitious sprouts were smaller and more susceptible to damage and decay than those arising from dormant buds. The authors speculated that if the same cutting height had been used for the second cutting, there would have been no decline in sprouting vigour.

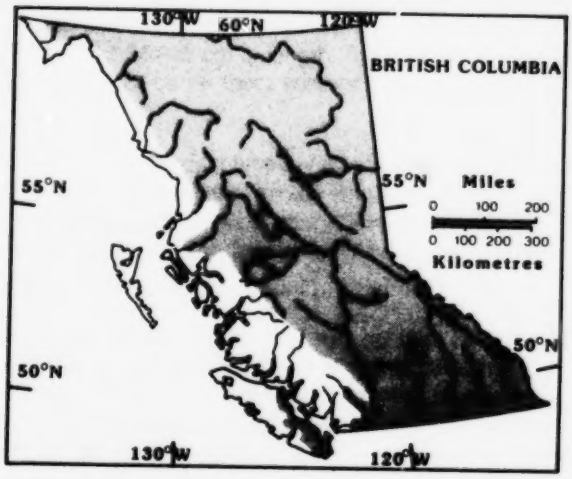
The same study found that sprouting vigour of eastern cottonwood (*P. deltoides*) was lowest when cutting took place early in the growing season, probably because food reserves were low after initiation of growth in spring.

Herbicides: In the mid-Skeena River area, cottonwood was susceptible to glyphosate applied as a late foliar spray at rates as low as 1 kg/ha (J. Pollack, pers. comm., Jan. 1985).

Soil Disturbance: Logging disturbance or mechanical site preparation that exposes patches of moist mineral soil can create an ideal seedbed for germination and survival of black cottonwood seedlings (Fowells (compiler) 1965). Stem or root fragments incorporated into moist mineral soil can be expected to regenerate, and damaged trees will produce new shoots.



Populus tremuloides (trembling aspen).



Distribution of *P. tremuloides* in British Columbia.

Populus tremuloides Michx. — Trembling aspen (quaking aspen)

DESCRIPTION

Trembling aspen is a small to medium-sized deciduous tree with a narrow dome-like crown that forms extensive clones by means of root suckering. It is commonly 6–12 m tall, but can reach 25 m in height. The bark, whitish to greenish grey with characteristic black scars, is smooth, but becomes furrowed at the base with age. Twigs are slender, reddish or grey, with long, pointed buds. Leaves are nearly round with a pointed tip, rounded teeth, and a flattened stalk that causes them to tremble in the breeze. The long, drooping male and female catkins appear on separate trees. Female catkins release many tiny, cottony seeds (Viereck and Little 1972; Brayshaw 1978).

Variation: Aspen is the most widely distributed native tree in North America (Brisette and Barnes 1984). Three poorly defined local varieties are recognized in British Columbia. The variety *vancouveriana* is found on Vancouver Island and adjacent coastal areas; var. *aurea* appears in the Cariboo region to the Rocky Mountains; and the typical var. *tremuloides* is widely distributed throughout the B.C. mainland (Taylor and MacBryde 1977; Brayshaw 1978). Because the species forms extensive, genetically identical, male or female clones, marked phenological or behavioural differences between adjacent clones can be easily observed (Fowells (compiler) 1965; Steneker and Wall 1970; Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Aspen occurs throughout B.C. east of the Coast Mountain Range. Variety *vancouveriana* is scattered throughout the Georgia Strait area, but northwards, aspen occurs only sporadically on the Coast where it has migrated westward along major river valleys. It is extremely abundant in the central and northeastern parts of the province, especially in the BWBS, SBS, and IDF biogeoclimatic zones, where it forms extensive stands (Brayshaw 1978; Krajina *et al.* 1982).

Altitudinal Range: Trembling aspen extends from valley bottoms to approximately 1200 m in the Interior and is occasionally found near sea level on the Coast (Lyons 1952). In interior Alaska it is confined to elevations below 900 m (Viereck and Little 1972).

HABITAT

Climatic Relations: The broad geographic distribution of this species indicates that it is adapted to a wide variety of climates. Cold continental and boreal climates appear to be more favourable than the humid, equable coastal environment, and the species is almost absent in cool perhumid areas. Towards the southern limits of its range in the U.S., it tends to be found at higher elevations in the mountains only, and in dry climates it may be restricted to protected habitats (Fowells (compiler) 1965). In northern B.C. and at high elevations it is most abundant on sunny, south aspects.

Site and Soil Conditions: Aspen can inhabit a wide range of sites including shallow rocky soils, loamy sands, and wet clays, but it is dominantly a species of well-drained uplands. Best growth is on moist but well-drained and porous, loamy soils; rockiness greatly limits stand development (Fowells (compiler) 1965; Steneker 1976; Burns (compiler) 1983). In B.C., trembling aspen occurs dominantly on luvisolic soils.

Nutrient Relations: Aspen is tolerant of poor soils but exhibits its best growth on nutrient-rich substrates, especially calcium-rich soils derived from limestone (Fowells (compiler) 1965; Krajina *et al.* 1982). However, studies in Wisconsin indicated that soil nutrient levels were of little importance in determining aspen site index (Fralish 1972). Aspen is regarded as a soil improver, particularly after fire (Fowells (compiler) 1965). It has high levels of potassium in its foliage, wood, bark, and litter relative to other northwestern tree species (Minore 1979), and redistributes great quantities of nutrients (especially calcium, magnesium, and nitrogen) to the surface soil layers through its litter (Fowells (compiler) 1965; Krajina *et al.* 1982). Biogenic cycling of calcium by trembling aspen is believed to maintain the luvisolic soils of the Fort Nelson area in a relatively productive state by retarding acid leaching (Valentine *et al.* (editors) 1978).

Water Relations: Aspen is abundant on sites ranging from xeric to hygric in moisture status, but best growth is found on sites with abundant moisture (Krajina *et al.* 1982; Angove and Bancroft 1983). Fralish (1972) indicates that soil moisture is the most important factor affecting the relative growth of aspen, and water tables between 1.0 and 2.5 m in depth are preferred, especially in coarse- and medium-textured soils. Aspen can survive long periods of flooding (Krajina *et al.* 1982)

Light Relations: Aspen is a shade-intolerant species that requires full sunlight for growth (Lutz 1955; Krajina *et al.* 1982). Strong light is needed to stimulate production of root suckers and ensure their continued, vigorous growth. Higher light intensities increase production of roots in young suckers (Fowells (compiler) 1965).

Temperature Relations: Frost resistance in aspen is high, and the species easily survives in frozen ground having no snow cover (Krajina *et al.* 1982). In the taiga of Alaska it is dominant on sites where the permafrost layer comes to within 20 cm of the soil surface (Foote 1983). Foliage is susceptible to late spring frosts (Strain 1966). Soil temperature is very important in the production of root suckers. Direct heat must reach the forest floor and temperatures must be 20–30°C for maximum production of root suckers (Fowells (compiler) 1965; Steneker 1976).

GROWTH AND DEVELOPMENT

Aspen is characterized by rapid early growth and a relatively short life-span. Although individual trees may live as long as 200 years, stands generally reach an advanced state of decay between 55 and 90 years. The tree develops a slender, limb-free trunk and a small crown.

The wide-spreading roots typically extend 1.0–1.5 m into the soil, but can penetrate to as deep as 2.2 m and may extend as far as 14 m from the stem base. Root development can be greatly hindered in rocky soils (Lutz 1955; Fowells (compiler) 1965; Maini 1972; Hosie 1973).

Aspen is most often seen in cutover or recently burned areas as small clumps of trees, each consisting of large numbers of root suckers (Schier and Campbell 1978). Sandberg (1951, cited by Schier and Campbell 1978) found that competition between the suckers usually reduces most clumps to a single stem by the 5th year and almost all to a single stem by the 10th year. Vigorous suckers may grow as much as 2 m in their 1st year, but subsequent height growth will average 30–60 cm annually (Steneker 1976). Seedling growth is much slower. Fowells (compiler, 1965) reports that growth in the 1st year averages 30 cm, while in Alaska, 3-year-old seedlings reached a maximum height of 27.5 cm (Zasada *et al.* 1981).

Phenology: Flowering takes place before the leaves appear in early spring (usually April or May). All trees within a clone develop their flowers simultaneously, although separate clones flower at different times. Male clones flower before females clones. The fruits mature as the leaves expand, and are normally ripe during May or June, about 4–6 weeks after flowering. Seed dispersal takes place shortly after ripening is complete, typically in the first few weeks of June. Within ecotypic zones, flowering period and time of seed maturity appear to be quite regular and differences in flowering time apparently depend on current temperatures (Fowells (compiler) 1965; Steneker and Wall 1970; Viereck and Little 1972; USDA 1974; Brayshaw 1978).

Leaf phenology is also identical for all trees within the same clone. Earliest and latest flushing clones within a given area may be 1–3 weeks apart in their phenological development, giving a patchwork appearance to an aspen stand, and making delineation of individual clones easy. There may also be several weeks difference in the timing of leaf fall among different clones (Steneker and Wall 1970).

In a provenance study located in Michigan (Brissette and Barnes 1984), clones from western North America initiated shoot growth earlier in spring than clones from Michigan, indicating that under native conditions, the western families are adapted to initiate growth at lower accumulated degree-days. Clones from northern latitudes or high elevations also ceased growth much earlier than the Michigan clones because they are genetically adapted to the photoperiods and growing season temperatures of their native habitats.

REPRODUCTION

Seed Production and Dispersal: Aspen begins to flower between 10 and 20 years of age. Flowers are typically unisexual, with male and female trees occurring in separate clones, but a small percentage of both male and female trees bear perfect flowers. The ratio of male to female trees is approximately 3 to 1 in natural populations in the eastern U.S. Pollen is wind-dispersed between clones. Female trees produce an adequate seed crop annually, with good seed crops every 4–5 years. The tiny cottony seeds can be carried several kilometres by wind (Fowells (compiler) 1965; Maini 1972).

Seed Viability and Germination: The viability of fresh fertile seed is high (Fowells (compiler) 1965), but seeds remain viable for only 2–3 weeks after maturity (Strothman and Zasada 1957). Reproduction does occur from seed (Maini 1972) but is rare, primarily because the short period of viability rarely coincides with environmental conditions that are sufficiently moist to allow seedling establishment (Barnes 1966).

Seed germination and seedling survival are best on moist mineral or humus seedbeds with moderate temperatures, good drainage, and little competition from other vegetation (Steneker 1976; McDonough 1979). Regeneration from seedlings is of minor significance as a means of reproduction in western North America (Fowells (compiler) 1965; Steneker and Wall 1970).

Vegetative Reproduction: The dominant form of regeneration in aspen is through suckers that develop from the extensive lateral root system (Steneker 1976; Schier 1981). Sprouts from the root collar or stump are uncommon but do occasionally occur (Maini 1972). Root suckers in Alaska appeared up to 25 m away from a fire-killed mature aspen, with the majority of the suckers occurring within 10 m of the stem base (Lutz 1955). Suckers normally originate from roots 0.75–2.2 cm in diameter in the upper 10 cm of the soil, but can appear on roots as deep as 28 cm (Kemperman 1978; Schier and Campbell 1978).

A few suckers will arise every year, even in undisturbed stands, but strong light and heat must reach the forest floor to stimulate vigorous suckering (Fowells (compiler) 1965). The optimum temperature range for suckering is 20–30°C (Steneker 1976). Suckers are initially dependent on the root system of the parent plant, but rapidly form their own root systems (Fowells (compiler) 1965).

Suckering produces extensive clones of genetically identical trees. Clones as large as 81 ha in size have been identified in western North America (Kemperman and Barnes 1976), but most clones are much smaller. Trees of different clones vary significantly in their suckering ability, phenology, growth rates, form, and disease susceptibility (Steneker and Wall 1970; Maini 1972). Age does not seem to affect suckering capacity, provided that the stand is not breaking up as a result of decay and old age (Steneker 1976).

PREDATION AND PESTS

Aspen is highly susceptible to various forms of decay and periodically suffers from major insect infestations. Principal disease and insect pests are outlined by Fowells (compiler, 1965).

Aspen has high palatability for cattle and sheep, and is browsed by moose, deer, and other wildlife species. Smaller mammals such as porcupines, mice, and hares do considerable damage by feeding on the bark (Sampson 1919; Fowells (compiler) 1965; McLean 1979).

EFFECTS ON CROP TREES

Competition: Aspen is considered a serious competitor with coniferous trees throughout the Interior of B.C., especially in the BWBS zone, where it is particularly well established. It rarely seeds-in to clearcuts, thus competition results from the suckers of trees already established prior to harvesting. The numbers of young suckers produced can be immense: a single tree in Alaska reportedly produced 36 230 suckers within 3 years (Lutz 1955). Aspen density and the rapid growth of young suckers provides young conifers with severe competition for root and crown space (Lees 1966). Suckers have the advantage of an established root system and always grow more rapidly than coniferous seedlings when open-grown (Jones 1974).

Conifers growing beneath an understory of aspen are also subject to significant mechanical damage (Kittredge and Gevorkantz 1929, cited by Steneker 1967). "Whipping" damage is particularly severe at approximately 55–75 years when understory trees begin to pass through the increasingly decadent aspen overstory (Lees 1966).

Beneficial Effects: Aspen is considered to be a site improver where burning or other forms of disturbance have reduced soil nutrient levels, because it returns large quantities of nutrients to surficial layers through its litter (Fowells (compiler) 1965; Krajina *et al.* 1982).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Trees cut or damaged during logging will produce prolific suckers. Even trees that remain undamaged will produce suckers as the root system is stimulated by the increased light and heat on the forest floor (Fowells (compiler) 1965). Suckers can grow up to 2 m in height during the first growing season following overstory removal (Steneker 1976).

Fire: Trembling aspen is adapted to an environment with recurring fires. The trees are susceptible to fire damage and may be severely scarred or killed outright, but subsequent colonization of the burned area through suckering is rapid (Fowells (compiler) 1965). Most suckers arise in the 1st year following a burn (Bailey and Anderson 1979). Burned areas typically produce more suckers than unburned areas because

high soil temperatures in the rooting zone stimulate root suckering. Burns of moderate to severe intensity can therefore produce more suckers than light burns (Horton and Hopkins 1965). The release of nutrients associated with burning may also stimulate the growth rate of suckers during the 1st year after a fire (Fowells (compiler) 1965).

Repeated burning is thought to promote suckering and result in denser stands (Fowells (compiler) 1965), but the regenerative capacity of aspen roots is not unlimited. A study by Buckman and Blankenship (1965) found that repeated spring burns eventually caused a significant reduction in sucker density.

Cutting: Cutting at any time of the year results in rapid regrowth of root suckers. Suckers appear immediately after cutting treatments carried out during the growing season, or early in spring after a dormant season cutting (Fowells (compiler) 1965; Steneker 1976). Cutting during the active season is believed to minimize the number of suckers (Fowells (compiler) 1965), but Steneker (1976) found that the effect of cutting season was negligible two or three seasons after treatment. Cut trees can produce more than twice as many suckers as girdled trees, and sucker growth from cut trees is superior (Schier 1978).

Where aspen trees were girdled within standing timber and the overstory was retained, death occurred within 4 years and no suckers were produced (Crombie 1965).

Herbicides: Glyphosate appears to be an effective chemical for controlling trembling aspen. Sutton (1978) reports that glyphosate was highly effective in killing aspen in Ontario at rates of 2.24 kg/ha and greater. When applied as a foliar spray at rates of 2.4–3.0 kg/ha near Prince George, glyphosate provided good to excellent control of aspen. Mortality rates were high and there was little suckering (Expert Committee on Weeds 1984).

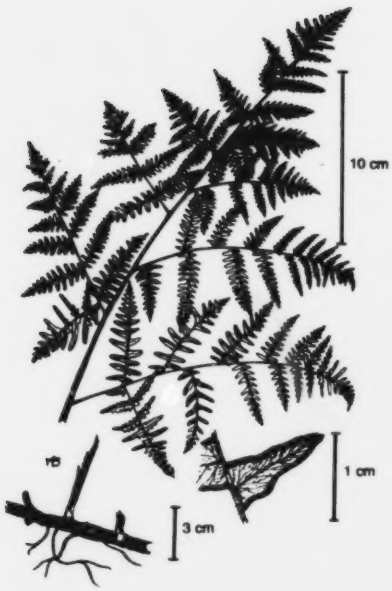
Hexazinone, applied as a liquid spray, by soil injection, or through granular applications also controlled aspen. However, results were variable in areas with deep organic layers (Expert Committee on Weeds 1984).

Both glyphosate, applied by hypohatchet (20% solution: 2 ml per 7.5 cm dbh), and hexazinone, applied by spot gun (pure: 8 ml per 2.5 cm dbh), killed or seriously injured all aspen trees in a New Brunswick study (Wile 1981).

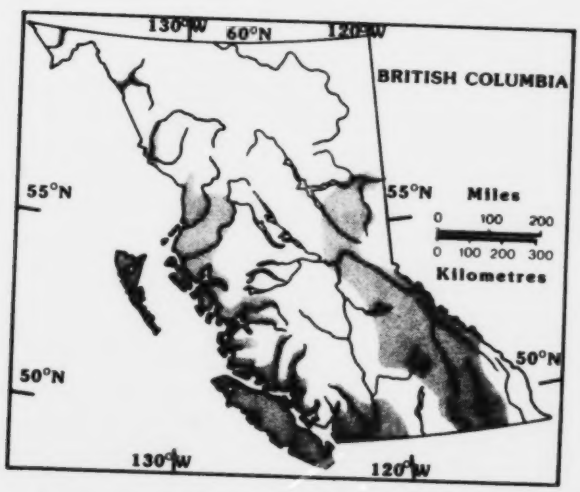
Results with 2,4-D have been variable. Steneker (1976) reports that 2,4-D, applied to the foliage from the air or ground, will kill all above-ground tree parts, but will not prevent suckering. Similar results were obtained by Bowes (1981) with a dormant spray of 2,4-D ester at 2.2 kg/ha; however, at 4.4 kg/ha, most aspen were killed and suckering was minimal. Basham (1982) found that after being sprayed with 1.4 kg/ha of 2,4-D, surviving aspen had reduced height and diameter growth, but within 6 years they had resumed normal growth rates.

Soil Disturbance: Site preparation methods such as scarification and discing that expose areas of mineral soil will increase suckering by increasing soil temperatures and light penetration in the rooting zone (Fowells (compiler) 1965; Jones 1974). Rows of suckers often appear along plowed furrows prepared for conifer regeneration (Fowells (compiler) 1965). A high level of cultivation that eliminates the aspen root system is needed for effective control. Deep plowing techniques that tear up the tree roots will reduce suckering. Better control of aspen regrowth may be achieved if mechanical site preparation is carried out during the growing season (Hoyles 1979).

Fertilization: Nitrogen fertilization significantly increases aspen foliar biomass and leaf area (Coyne and Van Cleve 1977).



Pteridium aquilinum (bracken).



Distribution of *P. aquilinum* in British Columbia.

Pteridium aquilinum (L.) Kuhn — Bracken

DESCRIPTION

Bracken is a large weedy fern with fronds that arise singly from an extensive creeping underground rhizome. The fronds are approximately 1–2 m tall with a stout, straw-coloured stipe (stem) and a triangular-shaped blade. The blade is three times pinnately compound; the final leaf divisions (pinnules) are leathery above and densely woolly beneath. The spores are borne in sori along the edge of the underside of the leaf (Taylor 1973*a*; Cody and Crompton 1975).

Variation: Bracken is a worldwide species with many geographic varieties. The western bracken found in British Columbia is described by Taylor and MacBryde (1977) as *Pteridium aquilinum* ssp. *aquilinum* var. *pubescens*. The biology, ecology, and control of bracken have been widely studied in Britain and elsewhere. British information on the autecology of bracken should apply well to var. *pubescens* in North America (Cody and Crompton 1975; D. Minore, pers. comm., Dec. 1984), but subspecies from New Zealand and other (sub)tropical areas behave differently since there is often no dormant season (Fletcher and Kirkwood 1979).

DISTRIBUTION AND ABUNDANCE

Bracken is one of the most widely distributed and successful vascular plants in the world (Page 1976). In B.C. it occurs along the entire length of the Coast and probably to approximately 56°N latitude in the Interior. It is most abundant in the CDF zone and adjacent drier subzones of the CWH on the south Coast, and in the ICH and IDF zones in southeastern B.C. Over the rest of the province its distribution is sporadic and poorly documented. In general, bracken is not abundant in areas where the natural vegetation is mostly undisturbed by man (Page 1976).

Altitudinal Range: Bracken has been found at over 1800 m in the Alps (Fletcher and Kirkwood 1979) and as high as 3250 m in the Colorado Rockies (Page 1976); but in B.C. it is rarely seen at high elevations (Taylor 1973*a*).

HABITAT

Climatic Relations: Around the world, bracken has successfully adapted to climates ranging from dry mediterranean to wet tropical (Gliessman 1976), but it is not present in hot and cold desert regions. The northern limit of its range is set, at least partially, by winter cold, and also by a minimum requirement for growing degree days above 5.6°C (Page 1976). Cody and Crompton (1975) summarize climatic conditions where bracken occurs in Canada as having mean temperatures ranging from as low as −15°C in winter to as high as 21°C in summer and precipitation ranging from 61 to 165 cm annually. However, precipitation is undoubtedly higher at some locations on the west coast of Vancouver Island where bracken exists. In B.C., bracken is not found over most of the boreal forest, nor in the driest areas of the province. It is most abundant in areas of humid climate, relatively mild winters, and a lengthy growing season.

Site and Soil Conditions: Throughout its range, bracken is associated with a wide variety of disturbed habitats such as old fields, burned areas, roadsides, bomb sites, and recent lava deposits. It is also found on undisturbed open forest and woodlands, in swamps and peat bogs (Cody and Crompton 1975; Fletcher and Kirkwood 1979). In Canada, bracken is found on podzolic and brunisolic soils (Cody and Crompton 1975). A study in Michigan (Hellum and Zahner 1966) indicated that best development occurs on deep glacial outwash sands of medium productivity, and poorest growth is on outwash sands of low productivity.

Nutrient Relations: Bracken is characteristically found on subacidic to acidic, nutrient-deficient soils. Its absence on nutrient-rich sites is apparently due not to an intolerance of high levels of nutrients, but rather to lack of opportunity or an inability to compete successfully with rich site vegetation (Hellum and Zahner 1966; Watt 1976; Fletcher and Kirkwood 1979). Nitrogen, phosphorus, potassium, and calcium are important for the growth of the sporophyte and it responds well to fertilization, especially with potassium and nitrogen (Watt 1976; Fletcher and Kirkwood 1979). In northern Idaho, bracken is significantly associated with soils having high levels of potassium (Mueggler 1965). However, nutrient status seems to be less important for growth of bracken than other environmental factors.

Carlisle *et al.* (1967) studied nutrient cycling in an oak woodland in Britain and concluded that *Pteridium* plays an important role in the woodland nutrient cycle. It contributes a significant percentage of soil nutrient

inputs through its litter and through foliar leachate. It is particularly important in potassium cycling, contributing 31.4% of the total potassium falling on the site. Other research indicates that the nutrient level of bracken litter is low relative to other species (e.g., 1% K, .0065% P), but the quality of the litter depends greatly on habitat conditions and frond vigour (Fletcher and Kirkwood 1979). Bracken produces prodigious quantities of litter and the rate of litter accumulation can exceed the rate of natural decay. Where this happens, the roots and rhizomes move upward in the soil so that the plant becomes progressively more dependent on nutrients contained within its own debris, and less on underlying mineral soil (Watt 1976).

Water Relations: In Canada, bracken grows on both moist and moderately dry sites, but its growth responds favourably to an abundant supply of soil moisture (Cody and Crompton 1975). On dry, shallow soils, fronds are sparse and short, and photosynthetic efficiency is much reduced as the plant adopts drought avoidance measures such as stomatal closure. It favours slightly shaded habitats such as woodlands and hollows where it is protected from drought and exposure. Growth is poor on waterlogged sites, presumably because of a lack of oxygen. The rhizome system is typically very shallow on such sites, but there are reports that bracken can survive in wet, poorly aerated soil by obtaining oxygen through the hollow stems of dead fern fronds (Watt 1976; Fletcher and Kirkwood 1979).

Light Relations: Bracken is considered to be semi shade-tolerant to shade-tolerant (Rowe 1983). It is adaptable to a wide range of light intensities, but is most often a colonizer of open land (Fletcher and Kirkwood 1979). In southwestern Oregon it was found at all light levels above 3% of full light, but only reached 75% or more of ground cover at 60–100% of full light (Emmingham 1972). Germination and satisfactory vegetative growth will occur under a wide range of light intensities, but spore production decreases significantly in the shade (Page 1976). Hellum and Zahner (1966) report that open- and shade-grown forms of the frond are somewhat different.

Temperature Relations: The fronds and rhizome buds of bracken are highly sensitive to frost and frost is a major factor limiting the latitudinal and altitudinal distribution of the species (Fletcher and Kirkwood 1979; Grime 1979). Late spring and early fall frosts may determine the length of the plant's growing season. Fronds that emerge early in the spring are frequently killed by frost and it is a major factor in fall senescence. Once fronds have safely emerged, heat requirements for growth are moderate (Watt 1976).

GROWTH AND DEVELOPMENT

Bracken is a highly successful and persistent plant because of its remarkable ability to develop from a single sporeling into a vast long-lived colony. The fern life cycle has been briefly outlined for *Athyrium filix-femina* (see page 51). In *P. aquilinum*, the mature fern sporophyte is actually an extensive clone with a massive underground system of stems.

Once the sporeling develops from the fertilized fern prothallus, it multiplies rapidly in size. By the second season of growth, there can be 45 fronds produced, by the third season as many as 126, and by the fourth season there can be 297 fronds (Conway 1952). What is visible above-ground, however, is merely a small fraction of the growth that is occurring underground.

The majority of the biomass of bracken exists as a system of creeping underground stems or rhizomes (Stanek *et al.* 1979). The rhizome system occurs on two levels. The lower level is situated deep beneath the soil surface (approx. 50 cm) and is responsible for storing food reserves and for lateral expansion of the colony. The upper level of rhizomes is located just beneath the soil surface. It produces numerous short shoots which give rise to the fronds and also has a network of fine roots for nutrient uptake (Cody and Crompton 1975; Fletcher and Kirkwood 1979).

Rates of growth of the rhizome vary from 5 to 200 cm per year. On average sites in Finland the rhizome spreads about 30 cm annually (Cody and Crompton 1975). Individual rhizomes as old as 72 years have been found, measuring 26 m in length from the young advancing front to the dying fronds at the rear of the colony (Watt 1940). Fronds as tall as 4.3 m have been measured in Great Britain (Watt 1976). Well-established colonies can have over 60 000 fronds per hectare (Hellum and Zahner 1966), and colonies have been known to survive for over 650 years (Fletcher and Kirkwood 1979).

Buds are formed on the ends of the underground short shoots in fall. Only a small percentage of these buds emerge in spring to form fronds. The majority of buds (as many as 120 000 per hectare) remain dormant, acting as a reserve to replace those fronds that are damaged or destroyed (Cody and Crompton 1975; Fletcher and Kirkwood 1979).

The rhizome system acts as a sink for carbohydrates. During the active growing season, developing fronds draw on these food reserves, and carbohydrate levels in underground stems are low. By midsummer the fronds begin to produce photosynthate, and carbohydrate levels are restored to high levels by September (Fletcher and Kirkwood 1979).

Phenology: Bracken emergence times are strongly controlled by spring temperatures (Hellum and Zahner 1966). In north temperate climates, frond emergence begins between March and early May, with maximum frond extension taking place in mid-May. If any emerging fronds are killed or injured during this time, replacement fronds will reappear up to mid-July (Cody and Crompton 1975). The growth rate of fronds following emergence is not related to the date of emergence. Thus, late-emerging fronds will be small at maturity compared with those emerging earlier (Hellum and Zahner 1966). Spores can be ripe as early as 22 July in B.C., but sporangia on any one frond do not mature simultaneously. Peak spore production occurs in late August and early September in Britain (Page 1976; Fletcher and Kirkwood 1979). Leaf senescence begins in August and is brought on by late summer drought and fall frosts. In the Pacific Northwest states, all fronds are dead by late October or early November (Gliessman 1976).

REPRODUCTION

Spore Production and Dispersal: Reproduction of bracken is by means of spores produced in sporangia on the underside of the pinnules (Cody and Crompton 1975). Spores can be produced by the second season of growth following germination (Fletcher and Kirkwood 1979). Approximately 64 spores are produced per sporangia (Conway 1957), so a single, well-developed frond may produce as many as 300 million spores. Not all fronds are spore-bearing and spore production varies enormously from locality to locality. During dry weather the spores are released by means of a natural dehiscence mechanism. The light spores are readily distributed by wind and can travel great distances. Spores are often brought to earth in the first fall rainstorm following the dry weather of late summer (Page 1976).

Spore Viability and Germination: Fern spores have remarkable viability and resistance to environmental extremes (Page 1979). Some fern spores have remained viable for as long as 48 years (Cody and Crompton 1975). Bracken spores have no dormancy requirements and can germinate within a few weeks of dispersal, but it is likely that most spores overwinter and germinate during moist spring weather. The spores will germinate in light or in darkness (Weinberg and Voeller 1969), and on a wide variety of substrates. Germination is frequently on disturbed habitats, and bare, sterile soil with a pH of 5.5–7.7 is ideal for germination. Germination is rarely observed in the field, and never occurs in an established bracken colony or under closed vegetation of any kind. It is clear that the primary role of spores is to allow the species to invade new habitats—not to maintain the colony within an established territory (Cody and Crompton 1975; Page 1976; Fletcher and Kirkwood 1979).

Vegetative Reproduction: In Canada and elsewhere, vegetative reproduction is the primary means by which bracken regenerates and expands in size within an established territory. When portions of an existing colony are destroyed, the colony will regenerate itself by rapid resprouting of dormant buds. New clones are created when the underground stem is broken off from the parent plant by decay or soil disturbance. Even extremely small fragments of stem will reproduce rapidly by producing new side branches (O'Brien 1964; Cody and Crompton 1975).

PREDATIONS AND PESTS

Cody and Crompton (1975) have produced a detailed summary of the major insect and microbial pests of bracken in Canada.

One reason for the remarkable success of bracken is that toxic chemical constituents in its foliage provide immunity against insect predators. Bracken is well known to be poisonous to domestic livestock and is believed to be a carcinogen. The degree of toxicity varies from region to region, but is apparently high in B.C. (Cody and Crompton 1975)

EFFECTS ON CROP TREES

Competition: Bracken has the ability to dominate a wide variety of vegetation types. Associated plants are severely inhibited and often excluded from the interior of bracken stands (Gliessman 1976). In the Pacific

Northwest states, bracken has been shown to prevent natural regeneration and retard growth of coniferous trees (Dimock 1964; Stewart 1976). The dense fern canopy, heavy litter, and extensive root and rhizome system provide severe competition for young conifers when bracken is well established on a site. Damage from above-ground vegetation includes shading, smothering, and mechanical damage (Gliessman 1976; Stewart 1976). Mechanical damage is especially severe in areas of heavy snowfall and on sloping sites where all stems fall in the same direction (M. Newton, pers. comm., Dec. 1984). The root and rhizome system competes directly with seedlings for moisture and nutrients; conifers may also be prevented from developing an adequate root system by the heavy layer of bracken litter (Cody and Crompton 1975; Gliessman 1976). In Britain, rabbits protected by the closed bracken canopy have been known to cause serious damage to other plants within the bracken stand (Gliessman 1976).

Allelopathy: Bracken is one of the better-known examples of a plant that produces toxic or growth-inhibiting chemicals to reduce competition from other plants. However, allelopathic effects on Douglas-fir and other conifers have not been unequivocably demonstrated. Gliessman (1976) believes that allelopathy is the primary mechanism by which bracken excludes its competitors in the Pacific Northwest. Stewart (1976) was able to demonstrate inhibition of germination and growth in thimbleberry and salmonberry, but Douglas-fir was relatively unaffected. Toxic chemicals are apparently released during early spring from litter, rhizomes, and roots (Gliessman 1976). Extracts from mature fronds do not contain inhibitory chemicals (del Moral and Cates 1971).

Beneficial Effects: Nicholson and Paterson (1976) examined the ecological implications of intensive bracken control in Britain and concluded that eradication of bracken would cause no significant negative impacts on the ecosystem. Nonetheless, in areas where no understory vegetation exists beneath the bracken, it can play a significant role in preventing soil erosion (Martin 1976). In some situations, the shading effect of bracken can be beneficial to other plants by creating a moister environment, free of drought stress (Gliessman 1976).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Bracken usually dies back or loses vigour as a forest canopy closes in. Removal of the forest cover creates suitable habitats for bracken invasion, particularly if areas are denuded of understory vegetation that might compete with bracken (Fletcher and Kirkwood 1979). In the CWH zone near Vancouver, bracken is able to expand quickly and increase substantially in dominance after canopy removal. Vigour, as measured by height, cover, and leaf area index, is significantly enhanced.[66] In the CDF zone on southeastern Vancouver Island, light thinning of Douglas-fir caused understory bracken biomass to increase by 3.8 times, while heavy thinning increased biomass by 8 times (Stanek *et al.* 1979).

Fire: Bracken is a fire-tolerant species whose reproductive strategy is adapted to periodic intensive fires. It is not only favoured by fire, but actually promotes fire by depositing a thick layer of highly inflammable litter on the ground every autumn (Isaac 1940). It is similar to fireweed in that it produces abundant wind-dispersed disseminules that allow it to invade a recently burned site at some distance from the parent population (Keeley 1981). It is known to invade recently burned areas in coastal B.C. (Lafferty 1972). Sterile burned soil is an ideal substrate for spore germination (Page 1976). Once established, bracken is favoured by extremely hot fires that kill other species whose roots and rhizomes are less well protected beneath the soil (Fletcher and Kirkwood 1979). Bracken vigorously produces new fronds following a fire (Tiedemann and Klock 1974; Cody and Crompton 1975; Rowe 1983) and its rhizomes spread quickly to take advantage of vacant niches (Fletcher and Kirkwood 1979). Bracken has become dominant in many areas along the Pacific coast that have been subjected to repeated fires (Isaac 1940).

Cutting: Manual and mechanical cutting methods have been widely used for bracken control in agricultural areas around the world. Bracken is very resistant to cutting, but treatments can be successful where they have been repeated at relatively short intervals over a period of several years. Timing of treatment is very important. The first cut should be made before the frond is fully expanded and the second should follow about 6 weeks later. In western Scotland, cutting 3 times a year completely eliminated bracken after 4 years, but cutting twice a year for 7 years was less effective.

[66] Brand, 1984.

Consecutive cutting treatments deplete rhizome food reserves, resulting in reduced height and density of fronds. Eventually food reserves are exhausted. The rhizome is rarely killed, however, and the potential for regeneration still exists. Special tools have been devised to "bruise" rather than cut the fronds, but opinion is divided on which treatment is more effective (Cody and Crompton 1975; Fletcher and Kirkwood 1979).

Herbicides: Virtually every herbicide known to man has been tested against bracken at one time or another. The history of these efforts is recounted in Chavasse and Davenhill (1973) and Fletcher and Kirkwood (1979). Effectiveness of different chemicals is extremely variable and regrowth is usually rapid. The object of chemical investigations is to find a herbicide that will translocate into the extensive rhizome system and destroy the dormant rhizome buds. Effects produced on fronds are a secondary consideration since any death of fronds will only stimulate more new fronds to emerge. The mode of action of herbicides on bracken is explained in detail by Fletcher and Kirkwood (1979).

Most literature cites asulam as the most effective herbicide for killing bracken without causing significant damage to crop species. Asulam is applied between July and September when fronds are fully emerged. Dichlobenil has been used effectively around young conifer trees in forestry plantations in Britain and New Zealand (Fletcher and Kirkwood 1979), and 2,4-D with sodium chlorate reportedly gave good control in Nova Scotia (Cody and Crompton 1975).

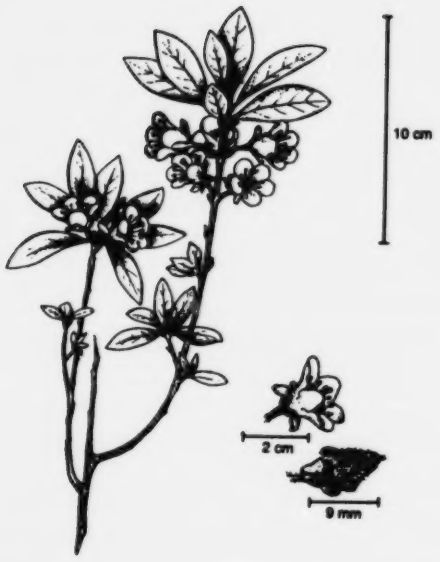
Recent reports suggest that glyphosate may be marginally more effective than asulam in controlling bracken in certain situations (Martin 1976). Late summer applications of glyphospate are very effective in Washington and Oregon (Wendel and Kochendorfer 1982; Conard and Emmingham 1984*a*). Near Prince George, glyphosate applied aerially in July at 2.25 kg/ha controlled 70% of the bracken after the first growing season (Expert Committee on Weeds 1984).

Soil Disturbance: Where soil and topography will allow, repeated deep plowing is the best method of bracken control (O'Brien 1964; Fletcher and Kirkwood 1979). Rotary cultivation is also effective, but is equally restricted by terrain and slash conditions. In areas of high summer rainfall, plowing and discing treatments may be less effective (O'Brien 1964).

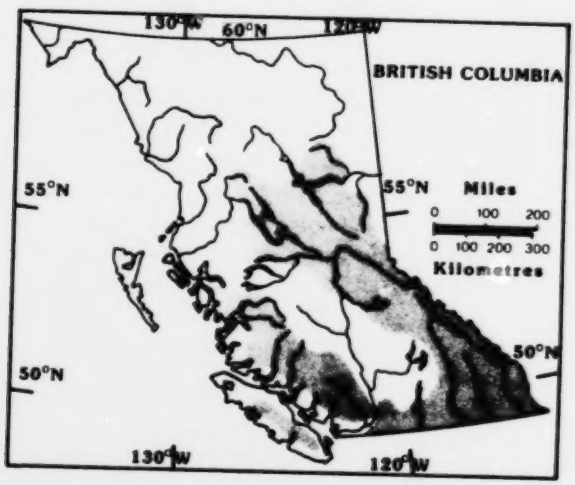
Fertilization: Roots and rhizomes of bracken respond to additions of nitrogen, phosphorus, potassium, and calcium by increasing the number of new fronds and rhizome branches initiated (Watt 1976). Where Douglas-fir was present as an overstory above bracken, fertilization lead to a decline in bracken biomass because it promoted growth of the tree canopy and reduced understory light (Stanek *et al.* 1979). The amount of nitrogen fertilizer tied up in bracken biomass was small and not considered to be critical to tree growth.

Other: Biological control of bracken has been investigated but does not at present appear to be feasible because the plant is susceptible to so few diseases. Cattle and pigs in fenced areas can be extremely effective in reducing frond density. Trampling by cattle is widely used as a means of control in agricultural areas.

In West Germany, sheets of gypsum board, fibreglass, and roofing paper have been used as a mulch to suppress frond growth around spruce trees (Fletcher and Kirkwood 1979).



Rhododendron albiflorum (white-flowered rhododendron).



Distribution of *R. albiflorum* in British Columbia.

***Rhododendron albiflorum* Hook.** **White-flowered rhododendron**
(white rhododendron, mountain misery)

DESCRIPTION

White-flowered rhododendron is an erect, slender-branched, deciduous shrub 1–2 m tall with shedding bark. Leaves are thin and narrow with loose rusty hairs. Flowers are white and showy, in clusters of one to four blossoms below the whorls of the leaves. The fruit is an ovate capsule (Szczawinski 1962).

Variation: No subspecies or varieties are described in British Columbia (Szczawinski 1962; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

White-flowered rhododendron is found in mountainous areas throughout B.C. to 57° N latitude, but its distribution is very scattered north of approximately 52° N. It is most abundant in the mountains of Vancouver Island, in the southern Coast Range, and in mountainous areas of southeastern B.C. (Szczawinski 1962). *Rhododendron albiflorum* is most abundant in the MH and wetter ESSF biogeoclimatic zones but also occurs in the AT, upper CWH and ICH zones, and rarely in the SBS zone.

Altitudinal Range: In the Coast Range, white-flowered rhododendron occurs mainly above 750 m (Lyons 1952) but may be found as low as 250 m on the west coast of Vancouver Island (Clark 1976). In the central Interior it occurs above 1200 m on the east side of the Fraser River and is scattered above 1500 m on the west side of the river (R. Coupé, pers. comm., Nov. 1984).

HABITAT

Climatic Relations: White-flowered rhododendron is a species of subalpine climates that have a short growing season and abundant snow. It is most abundant in areas of wet to moist climate where summer moisture deficits are uncommon. Its absence from the far north suggests that it may not be tolerant of extreme cold.

Site and Soil Conditions: *Rhododendron albiflorum* is a characteristic species of forested and open mountain slopes at or near timberline (Clark 1976). Parent materials are most often colluvial or morainal deposits and are frequently shallow to bedrock. Soils are most often Humo-Ferric Podzols, occasionally Dystric Brunisols, and have a Mor or Mormoder humus (see e.g., Mitchell and Green 1981; Coupé and Yee (editors)[67]).

Nutrient Relations: Most species of the genus *Rhododendron* are well known to favour acid soil (Szczawinski 1962; Clark 1976). Surface soil horizons in ecosystem associations with *R. albiflorum* as a dominant understory species typically have a pH of about 4.2 (see e.g., Brooke *et al.* 1970; Coupé and Yee (editors)[68]). Ecosystem associations with abundant rhododendron can range from very poor (oligotrophic) to very rich (eutrophic) in nutrients (see e.g., Klinka 1977*a*; Mitchell and Green 1981; Coupé and Yee (editors)[69]).

Water Relations: White-flowered rhododendron is described as occurring on wet or moist sites (Lyons 1952; Szczawinski 1962). However, within the ESSF zone of southern B.C., it is abundant on sites ranging from very rapidly drained (xeric) to very poorly drained (subhydric) (Angove and Bancroft 1983). In other areas of the province it tends to be most abundant on xeric and submesic sites (Klinka 1977*a*; Angove and Bancroft 1983; R. Coupé, pers. comm., Nov. 1984), but this may reflect its poor competitive ability in these areas rather than a preference for dry soil conditions.

Light Relations: White-flowered rhododendron is probably moderately shade-tolerant. It is abundant in partially shaded forest understories but does not grow well under dense forest canopies (W.R. Mitchell and D. Lloyd, pers. comm., Nov. 1984).

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

White-flowered rhododendron can reach heights of up to 2.5 m in favourable environmental conditions (R. Coupé, pers. comm., Nov. 1984). There is no information available on its morphological or physiological development.

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[67] Coupé and Yee (editors), 1982.
[68] Ibid.
[69] Ibid.

Phenology: Flowering occurs in late spring after the leaves have emerged (Lyons 1952). The growing season in its high elevation habitat is short, extending from June to August (Szczawinski 1962). Unlike most species of *Rhododendron, R. albiflorum* has deciduous leaves which turn spectacular shades of red and orange with the arrival of the first snows (Clark 1976).

REPRODUCTION

Seed Production and Dispersal: Virtually no information about the reproductive biology of *R. albiflorum* has been published. Seeds of members of the genus *Rhododendron* are typically minute (4–13 million per kilogram) (USDA 1974). The fruit of *R. albiflorum* is naturally dehiscent and the seeds have winged margins (Szczawinski 1962), indicating that seed dispersal is probably by wind.

Seed Viability and Germination: Seeds of the genus *Rhododendron* typically remain viable for approximately 2 years under very dry conditions. Most rhododendrons require light for germination but seeds have no chilling or scarification requirement (USDA 1974). The reproductive strategy of white-flowered rhododendron apparently does not involve the production of large numbers of seedlings, since seedlings are rarely observed in the wild and are not abundant in clearcut areas (R. Coupé and O. Steen, pers. comm., Nov. 1984).

Vegetative Reproduction: There is no indication that white-flowered rhododendron spreads by means of rhizomes. Like other, related shrub species, it is probably capable of resprouting from the root crown.

PREDATION AND PESTS

No information.

INTERACTIONS WITH CROP TREES

Competition: *Rhododendron albiflorum* is a major species of an Ericaceous *(R. albiflorum, Vaccinium* spp., *Menziesia ferrugina)* shrub complex in the ESSF and MH zones throughout much of southern B.C. This shrub complex dominates mesic and drier ecosystems in many high-elevation clearcut areas, but despite its abundance, virtually nothing is known about its effect on the regeneration and growth of conifers.

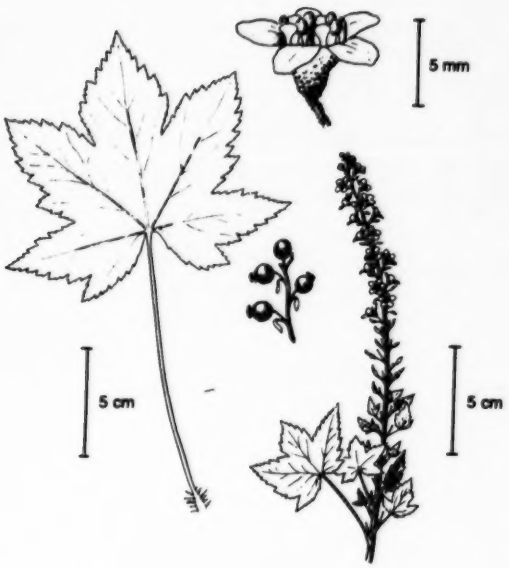
White-flowered rhododendron is capable of producing a very dense tangle of shrub growth (Lyons 1952), but its open habit and narrow leaves do not produce a deeply shading canopy. In the wet ESSFh subzone of the Cariboo Forest Region, it is possible that the major competitive effect on tree seedlings is the impact of shading on soil temperature (R. Coupé and O. Steen, pers. comm., Nov. 1984). Competition for soil nutrients may also limit tree growth, but in this subzone it is unlikely that competition for moisture is severe.

Del Moral and Cates (1971) showed that *R. albiflorum* has definite allelopathic potential in western Washington. Leaf — and especially litter — extracts inhibited growth of test plants in the laboratory, and field sampling showed that subordinate vegetation is markedly reduced beneath the rhododendron canopy.

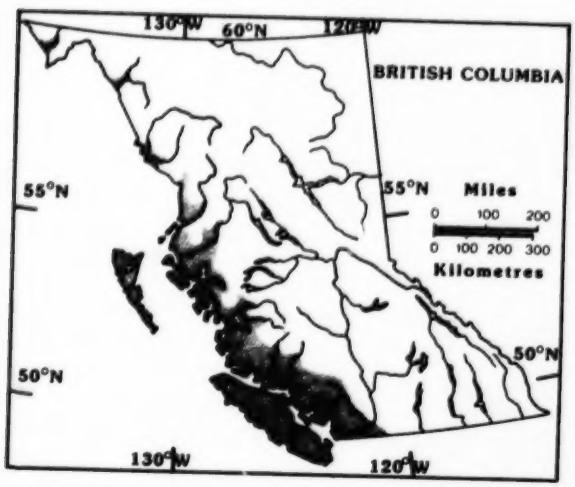
Beneficial Effects: On droughty, exposed sites, rhododendron may provide some shade and reduce evapotranspiration in young seedlings.

RESPONSE TO DISTURBANCE OR MANAGEMENT

There are no references in the literature to the response of white-flowered rhododendron to silvicultural practices or other forms of disturbance. The species is not seen as an aggressive, rapidly growing invader and it seems likely that damage from logging, mechanical site preparation, or prescribed burning will set the species back for several years (R. Coupé and O. Steen, pers. comm., Nov. 1984; M. Tanner, pers. comm., Jan. 1985).



Ribes bracteosum (stink currant).



Distribution of *R. bracteosum* in British Columbia.

Ribes bracteosum Dougl.

Stink currant
(blue currant)

DESCRIPTION

Stink currant is an erect to spreading deciduous shrub, 1–3 m tall. The twigs are coarse, unarmed with large red buds, and often have shredded bark. Leaves are large, palmate with five to seven pointed, toothed lobes and yellowish glands on the undersurface. Flowers and fruits are borne in long, erect racemes. The flowers are small, white to greeenish, and the fruit is a spherical berry with a glandular surface and a whitish bloom. The plant has a distinctly "skunky" odour (Viereck and Little 1972; Hultén 1974; Clark 1976).

Variation: No varieties or subspecies of *R. bracteosum* are described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Ribes bracteosum is found along the entire length of the Coast of B.C. including Vancouver Island and the Queen Charlotte Islands (Calder and Taylor 1968; Viereck and Little 1972; Hultén 1974). It is found occasionally on the east side of the Coast Mountains in southern and central B.C. but is never abundant (H. Roemer, pers. comm., Dec. 1984). Stink currant is most abundant in the CWH biogeoclimatic zone but is also found in the CDF, CCPH, and MH zones and is scattered in moister areas of some interior zones.

Altitudinal Range: Stink currant is primarily a species of low elevations, occurring near sea level along the Coast (Lyons 1952), but it does ascend to at least 1200 m in the MH zone of south coastal B.C. (Brooke *et al.* 1970).

HABITAT

Climatic Relations: The geographic range of stink currant suggests that it is a species of humid to perhumid climates with generally mild winter and summer temperatures.

Site and Soil Conditions: Throughout its range, stink currant occupies riparian or alluvial habitats or moist woods (Hultén 1974; Clark 1976; Campbell and Franklin 1979). In Alaska, it is frequently a pioneer of avalanche tracks, roadsides, windfall areas, and other disturbed sites where mineral soil has been exposed and the humus layer has had an opportunity to break down (Taylor 1932; Viereck and Little 1972). Soils on sites with abundant *R. bracteosum* are most often Regosols or Orthic Dystric Brunisols (see e.g., Yole *et al.*;[70] Banner *et al.*[71]).

Nutrient Relations: The preference of this species for alluvial habitats suggests that it has quite a high demand for nutrients. Ecosystem associations in which *R. bracteosum* is a characteristic understory species are most often classified as having a rich (permesotrophic) to very rich (eutrophic) ecological nutrient regime (see e.g., Banner *et al.*;[72] Yole *et al.*[73]).

Water Relations: In the Cascade Range of Oregon, *R. bracteosum* is almost always found near permanent water sources (Campbell and Franklin 1979). The authors speculate that summer drought probably prevents this species from colonizing hillsides adjacent to the riparian zone. In B.C., stink currant is typically associated with mesic to hygric sites that receive abundant supplies of well-aerated water through flooding or seepage flow (see e.g., Brooke *et al.* 1970; Yole *et al.*;[74] Banner *et al.*[75]).

Light Relations: Stink currant is most vigorous on open sites that receive abundant light but are not subjected to moisture stress (Taylor 1932; Viereck and Little 1972). In the forest it is typically found under open tree canopies or along streambanks where some sunlight is available.

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

There is no published information on the growth and development of stink currant. The form of the shrub is typically scraggly, and under favourable conditions it can reach over 3 m in height (Clark 1976). The average

[70] Yole *et al.*, 1982.
[71] Banner *et al.*, 1983.
[72] Ibid.
[73] Yole *et al.*, 1982.
[74] Ibid.
[75] Banner *et al.*, 1983.

height of the species is 1.5–2.5 m. When growing under open conditions, its large, palmate leaves can produce a dense, multilayered canopy, which probably allows very little light to penetrate.

Phenology: Stink currant flowers during May and June in coastal Alaska and fruits ripen between late July and August (Viereck and Little 1972). In the western Oregon Cascades, fruit dispersal was during August (Campbell and Franklin 1979). In the Kimsquit valley on the central B.C. coast, leaves had emerged by late April and were fully expanded by June (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.). Leaf senescence and abscission occurred between late July and mid-November in Oregon and at Kimsquit. Stink currant was one of the first species in the riparian community to begin losing its leaves, but the rate of abscission was slower than for most other species (Campbell and Franklin 1979).

REPRODUCTION

Seed Production and Dissemination: The fruit of species of the *Ribes* genus is a glandular berry that is dispersed almost entirely by birds and mammals during summer and fall (USDA 1974).

Seed Viability and Germination: Seeds of most species of the *Ribes* genus require a long period of chilling and in some cases an acid scarification treatment before germination can occur; however, each species seems to have its own unique germination characteristics. In nature, germination typically occurs in the spring of the year following ripening of the seed, after the seed has passed through the intestines of the bird or mammal vector. The best seedbed for germination of *Ribes* seed appears to be moist mineral soil that is well supplied with humus (USDA 1974).

These general comments on *Ribes* seeds seem to correspond well with field observations of *R. bracteosum*. Propagation by seed is believed to be the most important form of reproduction in this species (M. Newton, pers. comm., Dec. 1984). Species of the genus *Ribes* are known to be seed bankers (Rowe 1983).

Vegetative Reproduction: Most species of *Ribes* can be readily propagated using cuttings taken during the dormant season (USDA 1974). *Ribes bracteosum* apparently does not spread by means of root or rhizome suckers but it will sprout back from the root crown if damaged. Natural layering may also occur (M. Newton, pers. comm., Dec. 1984).

PREDATION AND PESTS

The fruit of stink currant is eaten by many bird species. Bears are also known to browse on the fruit and foliage (T. Hamilton, pers. comm., Jan. 1985).

Stink currant is an alternate host for *Cronartium ribicola*, the white pine blister rust (Foster and Wallis 1974).

EFFECTS ON CROP TREES

Competition: Stink currant is a common member of the complex brush community found on alluvial ecosystems along the coast of B.C. These brush communities pose some of the most serious vegetation management problems in B.C. because they occupy the most productive sites for coniferous tree growth and because competition to conifers is extremely severe.[76] *Ribes bracteosum* is not considered to be a major competitor in these coastal brush communities on the south Coast (Brand;[77] M. Scott and G. Kennah, pers. comm., Nov. 1984); however, on the central and north Coasts, it is one of the more abundant species on alluvial sites and can be a significant competitor (M. Geisler, pers. comm., Jan. 1985).

Stink currant does not grow or spread rapidly compared with other seral shrub species found on coastal alluvial sites (M. Newton, pers. comm., Dec. 1984), but where it is established prior to logging, or where planting is delayed for several years following disturbance, the species can impede conifer regeneration. Competition on these moist, rich ecosystems is probably primarily for light.

Because it acts as an alternate host to the white pine blister rust, stink currant is an important limiting factor to the regeneration of western white pine on the south Coast.

Beneficial Effects: No information.

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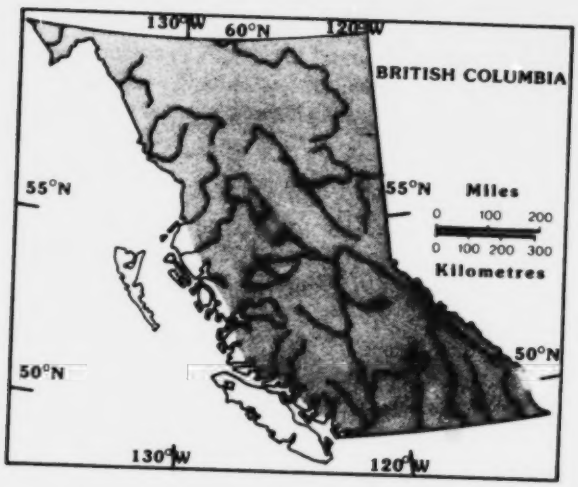
[76] A. Macadam, J. Pollack and R. Trowbridge. 1984. Trials of prescribed fire for vegetation management. The rehabilitation of coastal alluvial sites in the Prince Rupert Region (EP 885.03). B.C. Min. For., Smithers, B.C. Unpublished draft.

[77] Brand, 1984.

RESPONSE TO DISTURBANCE OR MANAGEMENT

There is little information regarding the response of stink currant to common silvicultural practices or other forms of ecosystem disturbance. Stink currant undoubtedly increases in size and vigour following canopy removal, as long as removal of shade does not impose significant drought stress. It resprouts following cutting or fire, but does not spread aggressively by vegetative means (M. Newton, pers. comm., Dec. 1984). Scarification of alluvial sites that produces a moist, mineral soil seedbed will favour germination of currant seeds (USDA 1974). Glyphosate at 2.0 kg/ha was successful in controlling stink currant in the Prince Rupert Forest Region (J. Pollack, pers. comm., Jan. 1985).

Rubus idaeus (red raspberry).



Distribution of *R. idaeus* in British Columbia.

***Rubus idaeus* L.** **Red raspberry**
(R. idaeus var. strigosus)

DESCRIPTION

Red raspberry is a deciduous shrub with erect, biennial stems arising from a perennial, subterranean, branching rhizome. The aerial stems, also known as canes, are 1–2 m tall with numerous bristles, prickles, and hairs. In the 1st year the canes are vegetative only, in the 2nd year they have flowering lateral branches. The leaves of raspberry are compound with three to seven irregularly shaped, toothed lobes. The inflorescence contains one to four white flowers. The fruit is the familiar raspberry, an aggregate of many small, red drupelets (Viereck and Little 1972; Hultén 1974; Whitney 1982).

Variation: Red raspberry is a variable species with many geographical and cultivated varieties across the northern hemisphere (Viereck and Little 1972). The red raspberry of British Columbia is described as *R. idaeus* ssp. *melanolasius* (Taylor and MacBryde 1977; Hultén 1974). Much of the research into the physiological development of this species has used cultivated varieties of raspberry that may differ significantly from the wild North American plant.

DISTRIBUTION AND ABUNDANCE

Red raspberry is found throughout B.C. except west of the Coast Mountain Range (Taylor 1973). It does not occur naturally on the Queen Charlotte Islands (Calder and Taylor 1968) nor on Vancouver Island where it may exist occasionally as a garden escapee (H. Roemer and A. Češka, pers. comm., Nov. 1984). Red raspberry is found in all biogeoclimatic zones except the CCPH, MH, and AT, but is rare in the PPBG and only occurs in eastern portions of the CWH and CDF zones. It is most abundant in moist areas of the Interior, and is uncommon in the dry areas of the southern Interior and west of the Fraser River in the central Interior (Angove and Bancroft 1983; R. Coupé, pers. comm., Nov. 1984).

Altitudinal Range: Red raspberry ranges from inland valley bottoms to subalpine elevations near timberline.

HABITAT

Climatic Relations: The broad distribution of this species across continental North America indicates that it is tolerant of a wide range of northern temperate climates, and not limited by the short growing season and cold winter temperatures of the boreal forest. Its absence from the Pacific coast suggests that it is poorly adapted to a perhumid environment with little annual temperature variation. Red raspberry is also absent from the hottest, most arid areas of B.C. (Angove and Bancroft 1983). In the Pacific Northwest states, tall raspberry canes are easily damaged by wind and rain (Williamson *et al.* 1979).

Site and Soil Conditions: Throughout its range, red raspberry is a species of disturbed sites, such as roadsides, burned areas, and openings and borders of forests (Wright 1972; Viereck and Little 1972; Taylor 1973*b*; Whitney 1982). It is rarely found within undisturbed, mature forest.

Nutrient Relations: Red raspberry's preference for recently disturbed soils suggests that it may have a relatively high demand for soil nutrients. Swedish research indicates that raspberry requires and accumulates large quantities of nitrates in its tissues where it invades recently burned sites (Wright 1972). Whitney (1982) has speculated that raspberry's reproductive strategy is adapted to take advantage of high initial levels of soil nitrates during the first years of establishment following disturbance. As soil nitrate levels decrease, the plant may shift from vegetative growth to seed production in response to a change in the carbon/nitrogen ratio of plant tissue. In the SBS zone near Prince George, red raspberry was found on sites with moderately high rates of available calcium and magnesium, but appeared to have a relatively broad ecological amplitude with respect to these nutrients. It was absent from sites with low nutrient availability (Wali 1969). Pojar *et al.* (1982) also indicate that in the SBS zone raspberry prefers sites with at least a moderate level of soil nutrients, but it can be found on nutrient-poor sites in the wettest subzones of southeastern B.C. (Comeau *et al.* 1982).

Water Relations: In areas of dry climate, red raspberry is restricted to receiving sites where seepage water augments the supply of soil moisture. In moister regions it is abundant on mesic sites and occupies a broad range of soil moisture regimes (Comeau *et al.* 1982; Pojar *et al.* 1982; Angove and Bancroft 1983). Best growth typically occurs on moist (subhygric) sites. Late summer drought reduces stored carbohydrate levels in the plant (Crandall *et al.* 1974), and may thereby result in lower plant vigour.

Light Relations: Red raspberry is a species of open, early seral conditions and is rarely, if ever, found under a closed forest canopy. It is described as fairly shade-intolerant by Whitney (1982). Whitney reports that with increased shading, raspberry dies out and puts more energy into fruit production.

Temperature Relations: The distribution of red raspberry indicates that it is a highly frost-tolerant species. Whitney (1982) reports that primocanes (canes in their first growing season) are more frost-hardy than floricanes (flowering canes in their second season). The overwintering flower buds require a certain period of cold to break dormancy and after mild winters flower buds sometimes fail to develop (Hudson 1959).

GROWTH AND DEVELOPMENT

Rubus idaeus has a complex developmental cycle that has been studied in detail by Hudson (1959) and Williams (1959) in Britain, and Whitney (1978, 1982) in the northeastern U.S. The natural habit of the species is to form dense colonies of short-lived aerial shoots that arise from a long-lived perennial root system. The following description of the morphological development of the raspberry plant is taken primarily from Hudson (1959).

When a young raspberry plant develops from seed, underground buds are formed in large numbers on the roots. These buds elongate, sending suckers to the soil surface, where they rest in a dormant state. The subterranean sucker can be as long as 50 cm. When conditions are favourable for growth, the shoot rapidly elongates, forming a new cane. At the same time, adventitious roots are produced at the base of the sucker.

During the first growing season in its 2-year life span the cane is known as a primocane. The primocane produces no flowers or fruit. It normally reaches a height of between 1.5 and 2 m, but total height growth is dependent on environmental conditions. In the laboratory or in favourable climates such as in New Zealand, canes can grow much taller. Towards the end of the growing season the primocane ceases to elongate and initiates the fruiting buds.

The 2nd-year cane (floricane) begins to grow in spring, following a suitable period of winter cold. The fruiting buds elongate to form lateral branches bearing both leaves and flowers. After fruiting is completed in late summer, the floricane dies back to ground level.

New primocanes emerge from the soil simultaneously with the maturation and death of the floricanes, repeating the 2-year cycle of growth. As successive shoots die back over a period of years they form a perennial woody rootstalk known as the stool. New shoots arising from the stool complete the same life cycle as shoots arising from root suckers.

Whitney (1982) studied the development of a raspberry stand or clone in the northeastern U.S. The first 2 years of life of the clone constitutes a building phase during which there is a rapid increase in the numbers of canes. Beginning in the 3rd year, a process of self-thinning occurs. The average number of suckers produced drops and the survival of suckers declines. As stand density decreases, net biomass production increases, peaking during the 4th year of stand development. As the stand matures, food resources are channelled towards seed production rather than vegetative growth. In the northeastern U.S., few stands persist for more than 5 to 12 years before they are replaced by other longer-living species.

Phenology: In Britain, root suckers elongate beneath the soil surface between August and April when above-ground parts are inactive but soil temperatures are warm enough to permit growth (Hudson 1959). In eastern Washington, flower buds were visible on 19 May and fruits were ripe by 2 July (Crandall *et al.* 1974). In Alaska, flowering occurs during June and July with fruit maturation occurring between July and September (Viereck and Little 1972). Leaf senescence in the floricanes coincides with fruit maturation. Primocanes retain their leaves much longer than floricanes (Whitney 1982).

REPRODUCTION

Seed Production and Dispersal: Rubus idaeus has perfect flowers with a floral structure adapted for pollination by bees (Faegri and van der Pijl 1971; USDA 1974). Wild plants are almost exclusively self-infertile (Keep 1968). Production of seed in a vigorous colony is prodigious. Approximately 70–90% of flowers eventually produce mature fruit. Good crops of fruit are produced nearly every year, but total production depends on environmental conditions (USDA 1974) and is also influenced by the stage of stand development. Towards the latter stages of development of the raspberry clone (approximately 4–12 years after establishment), progressively larger proportions of stored food reserves are devoted to seed production (Whitney 1982).

The fruit ripens unevenly over a period of several months, with each drupelet producing a single nutlet. Natural dispersal of the seed is by birds, small mammals, and bears (Ahlgren 1960; USDA 1974).

Seed Viability and Germination: The seeds of red raspberry remain viable for an extended period of time, probably in excess of 50 years (Whitney 1982). This lengthy period of viability allows the species to bank seeds in the soil where they can remain dormant until conditions become suitable for germination and seedling survival. Raspberry seeds require a lengthy period of chilling (approximately 120 days) before they will germinate, and in some varieties acid treatment also helps to improve germination. Light also helps to stimulate germination following chilling. Temperatures of between 10 and 25°C are favourable for germination (Jennings and Tulloch 1964; USDA 1974). Germination of stored or recently deposited seed is the primary means by which raspberry is able to become established on recently disturbed sites, but 1 year after stand initiation, further seedling establishment is almost nonexistent (Whitney 1982).

Vegetative Reproduction: Once red raspberry is established on a site, its ability to rapidly colonize the area depends primarily on its ability to reproduce vegetatively (Keep 1968; Whitney 1982). Formation of root suckers is the primary means of vegetative spread. Suckers develop into independent stools as intervening roots between the parent plant and the root sucker die off (Hudson 1959). Raspberry will regenerate readily from root cuttings taken during the dormant season, while cuttings taken between May and August usually fail to regenerate successfully (Williams 1959).

PREDATION AND PESTS

Fruits of red raspberry are one of the favourite summer foods of wildlife. Raspberries are important to many species of game birds and song birds, and are also eaten by small mammals such as raccoons, chipmunks, and squirrels. Deer and rabbits make extensive use of leaves and stems (Core 1974). Bears also browse on the fruit and foliage (Ahlgren 1960).

Williamson *et al.* (1979) describe some of the important insect and disease problems of cultivated raspberries, but many of these pests may not occur in Canada.

EFFECTS ON CROP TREES

Competition: Red raspberry is an abundant species on clearcut and burned areas throughout most of the Interior of B.C. It is an aggressive invader that frequently forms an almost monospecific shrub layer during the first 3–5 years following large scale disturbance (Whitney 1982). Its abundance and aggressive behaviour enable red raspberry to pre-empt a site's resources and make it an important competitor with coniferous tree regeneration in many moist areas of the Interior. Because red raspberry is usually not present prior to canopy removal, it rarely becomes a significant factor in clearcut areas until 3–5 years following logging (Eis 1981; C. Delong, pers. comm., Nov. 1984).

Red raspberry's mode of competition with conifers is not discussed in the literature. It undoubtedly includes shading and mechanical damage to young seedlings on sites where raspberry is dense and vigorous, and competition for moisture and nutrients on most sites. Competition is limited to the early stages of conifer stand establishment, since raspberry colonies are quickly eliminated once trees and shrubs begin to cast overhead shade (Core 1974; Whitney 1982).

Beneficial Effects: Possible beneficial effects of red raspberry on coniferous tree growth include its ability to reduce soil erosion on disturbed sites (Core 1974) and its ability to limit invasion of taller, longer-lived deciduous species during the early stages of succession.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Red raspberrry is a pioneer species that depends on forest openings for establishment and survival. It is known to rapidly invade clearcut areas (Whitney 1982). In the SBS zone north of Prince George, raspberry established itself on three of four site types within 6 years following logging (Eis 1981). Eis speculated that seeds were brought into a clearcut site by birds, but it is also probable that canopy removal provides suitable microsites for germination of long-buried seed. Red raspberry does not compete well with established understory vegetation and will not invade the moist productive Alluvial site type where a diverse shrub layer is already well established prior to canopy removal.

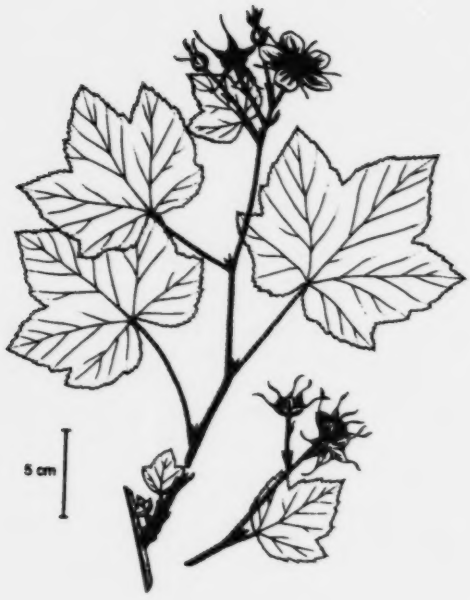
Fire: Seedlings of *R. idaeus* often appear in high densities after a fire, and the species is consistently more abundant on burned than on unburned areas (Wright 1972). In northeastern Minnesota where red raspberry was present prior to a fire, reproduction was primarily vegetative with only minor seedling establishment (Ahlgren 1960). Ahlgren speculated that vegetative parts of the plant must be very resistant to heat damage. In Alaska, raspberry plants were present the 1st year after fire on most areas studied by Foote (1983). Some studies from the northeastern U.S. report that cover and vigour begin to decline by the 3rd and 4th years following a fire (Wright 1972), while others find that it takes at least 5 years for raspberry to become dominant on a site (Ahlgren 1960). In B.C., red raspberry is frequently found in great abundance on sterile mineral soil that has been exposed by a very hard burn (R. Coupé, pers. comm., Nov. 1984).

Cutting: Most references to the response of red raspberry to cutting involve cultural attempts to improve fruit production rather than efforts to reduce the plant's vigour. Because raspberry canes are short-lived and perennial parts are situated underground, a single cutting of the canes will provide negligible control of the plant over the longer term. New shoots will rapidly be produced from root suckers and stools (Core 1974). Treatments that reduce the density of canes will serve to improve the vigour of remaining canes (Lawson and Waister 1972*a*; Crandall *et al.* 1974). Repeated heavy cutting will probably result in a depletion of stored food reserves and an eventual decline in the number and vigour of canes produced.

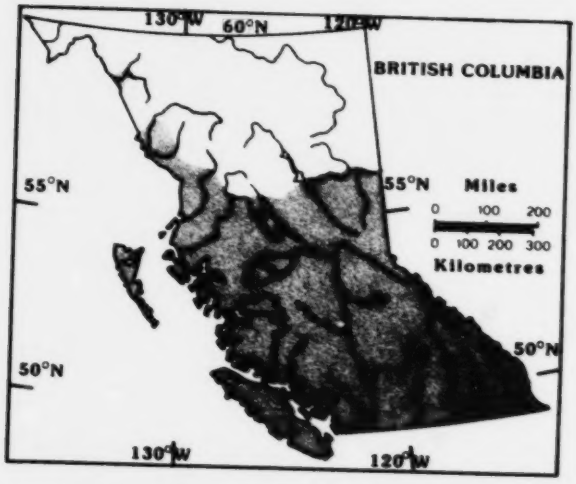
Herbicides: Red raspberry was found to be moderately tolerant of glyphosate applied as a foliar spray at 2.25 kg/ha near Prince George. It also appears to be quite sensitive to hexazinone applied at rates of 2–5 kg/ha (Expert Committee on Weeds 1984). Other herbicide applications reported in the literature involve efforts to control weeds and raspberry suckering in raspberry plantations. Simazine applied basally during the dormant season causes no injury to raspberry plants at 2 kg/ha. Paraquat/diquat applied before budbreak gives partial control of sucker growth, best control is achieved if suckers are less than 15 cm at the time of treatment (Lawson and Waister 1972*a*). Dinoseb is used to dessicate young primocanes but is not translocated below ground and has no effect on replacement canes (Williamson *et al.* 1979)

Soil Disturbance: Raspberry will rapidly invade areas of bare disturbed soil where there is little competition from other plant species (Keep 1968; Whitney 1982). Where mechanical site preparation is used within existing stands of raspberry, soil disturbance can fragment the root system, creating new independent stools (Hudson 1959) and stimulating root suckering (Core 1974). Repeated cultivation of the soil will control the spread of raspberry by root suckering, but this will be accompanied by an increase in the vigour of adjacent undisturbed plants (Lawson and Waister 1972*a*).

Fertilization: Application of nitrogen fertilizer to red raspberry can either increase suckering and have no effect on height growth, or increase height growth without affecting stand density (Lawson and Waister 1972*b*). Lawson and Waister also observed increased levels of winter mortality following fertilization. This injury may be due to a delay in the onset of dormancy (Jennings and Cormack 1969, cited by Lawson and Waister 1972*b*) or to increased incidence of disease in fertilized plants (Goode 1970, cited by Lawson and Waister 1972*b*).



Rubus parviflorus (thimbleberry).



Distribution of *R. parviflorus* in British Columbia.

Rubus parviflorus Nutt. — Thimbleberry

DESCRIPTION

Thimbleberry is a deciduous shrub with relatively short-lived stems or canes and an underground network of rhizomes. The canes are erect to semi-prostrate, without prickles and 1–2 m tall. The leaves are large, maple-shaped with 3–5 toothed lobes and a soft crinkly surface. The conspicuous, white-petalled flowers are borne in a broad, irregularly shaped infloresence. The soft, thimble-shaped red fruit is an aggregate of many small, hairy drupelets (Viereck and Little 1972; Taylor 1973*b*; Clark 1976; Marchant and Sherlock 1984).

Variation: Thimbleberry is a highly variable species (Hultén 1974) with several recognized subspecies. Only the typical ssp. *parviflorus* is found in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Thimbleberry is common throughout B.C. to approximately 56°N latitude in the Interior and along the entire length of the Coast including Vancouver Island and the Queen Charlotte Islands. It is absent from the SWB biogeoclimatic zone and from the BWBS outside of the Peace River valley. Otherwise, thimbleberry is found in all forested biogeoclimatic zones. It is most abundant in the CWH zone and in wet subzones of the Interior and is very rare in the PPBG and in other dry areas of the south and central Interior.

Altitudinal Range: Thimbleberry ranges from sea level to over 900 m on the Coast and from valley bottoms to over 1200 m in the Interior (Lyons 1952; Taylor 1973*b*).

HABITAT

Climatic Relations: Thimbleberry is apparently tolerant of a wide range of climatic conditions in B.C., but it is poorly adapted to survive the extremely cold winters and short growing seasons of the boreal region. It appears to favour a moist to wet climate and does not tolerate extreme summer moisture stresses such as can be encountered in the driest areas of the southern Interior. In northern Idaho, Irwin and Peek (1979) report that thimbleberry is more abundant on northerly slopes, while Mueggler (1965) found it occurring equally on north- and south-facing slopes. Brand considers that in south coastal B.C. it favours sites with a drier, warmer and more continental microclimate than those favoured by salmonberry.[78]

Site and Soil Conditions: Thimbleberry grows on a wide variety of soils and landforms both in wooded areas and on disturbed sites. It is common beneath open forest, on roadsides, in cutover areas, on avalanche tracks, and in riparian habitats (Viereck and Little 1972; Taylor 1973*b*; Gratkowski 1978; Gilbert 1980). Ecosystem associations with thimbleberry as a dominant understory species occur widely in the SBS, ICH, and ESSF zones on morainal, fluvial,and lacustrine parent materials with Luvisol, Brunisol, or Podzol soils (see e.g., Pojar *et al.* 1984; Coupé and Yee (editors);[79] Delong *et al.*[80]). In the CWH zone, thimbleberry is most abundant and vigorous on fluvial sites.

Nutrient Relations: Thimbleberry appears to have a relatively broad tolerance for nutrient levels. In the SBS zone it is found on sites with a wide range of available calcium (Wali 1969) and with ecological nutrient regimes ranging from moderately poor to very rich (Pojar *et al.* 1982). On the south Coast, thimbleberry grows well on medium to nutrient-rich sites.[81]

Water Relations: Thimbleberry is most abundant and vigorous on moist, well-aerated soils with a subhygric moisture regime, although it occurs on sites with a very wide range of moisture regimes (Pojar et al. 1982; Angrove and Bancroft 1983). It is common on relatively dry hillsides but on these sites it tends to be a much smaller shrub than where moisture is abundant (Clark 1976; Marchant and Sherlock 1984). It does not grow well on wet, poorly drained soils.[82]

Light Relations: Thimbleberry can be found under closed deciduous or coniferous forest canopies, but it is most abundant and vigorous under at least partially open conditions (Gilbert 1980; Brand[83]). In south-western Oregon, thimbleberry is found at all light levels down to below 3.5% of full light, but it has greatest

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[78] Brand, 1984.
[79] Coupé and Yee (editors), 1982.
[80] Delong *et al.*, 1984.
[81] Brand, 1984.
[82] Ibid.
[83] Ibid.

cover at 60-100% of full light (Emmingham 1972). Studies of photosynthetic capacity carried out in Washington indicate that thimbleberry is less shade-tolerant than salmonberry (Barber 1976). Barber used this evidence to explain why thimbleberry is never abundant in the understory of red alder stands in the Pacific Northwest states. However, on the north Coast of B.C., thimbleberry is often one of the dominant understory species beneath red alder (J. Pollack, unpublished data, 1984, B.C. Min. For., Smithers, B.C.). These conflicting data may indicate a difference in shade tolerance of thimbleberry under different environmental conditions, or they may indicate that presence or absence of thimbleberry is due not so much to light availability, as to relative competition from other plant species.

GROWTH AND DEVELOPMENT

There are no studies of the growth and development of the thimbleberry plant. It is known to be a strongly rhizomatous species that, like other *Rubus* species, produces relatively short-lived canes. Viereck and Little (1972) describe the canes as perennial. Our observations of a small number of plants in west central B.C. indicate that the canes are dominantly biennial, with flowers and fruit produced on short lateral branches in the 2nd year. Some of the canes survive for at least 3 years, producing large lateral branches.

When open-grown, thimbleberry produces a dense multilayered canopy and has a very large leaf area.[84] Its photosynthetic capacity in full light is therefore higher than that of other associated species (Barber 1976). This high photosynthetic efficiency enables it to achieve rapid initial height growth. Brand observed that maximum height growth occurs by the second or third growing season following establishment.[85]

Phenology: In western Oregon and Washington, vegetative buds of thimbleberry can become active as early as late February (Stewart 1974*b*). In northern Idaho and western Montana, bud burst takes place between early April and early June depending on elevation and weather conditions. Leaves are fully grown approximately 1 month after bud burst. Leaf senescence typically begins by late August in Idaho and Montana and leaf fall extends from late August to mid- to late October (Schmidt and Lotan 1980). Data from the central coast of B.C. indicate similar timing of vegetative events. (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.).

Flowering can extend from early May to early August, but is centred on the months of June and July both in Alaska (Viereck and Little 1972) and in Idaho and Montana (Schmidt and Lotan 1980). In B.C., fruits ripen from early June to mid-September depending on elevation and other local factors (Marchant and Sherlock 1984; T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.).

REPRODUCTION

Seed Production and Dispersal: The berry-like fruit of thimbleberry contains many small seeds. Seed production can be sparse at high elevations. Once ripe, the fruit fall readily to the ground (Marchant and Sherlock 1984). Wider dispersal of the seed is primarily by birds (Core 1974; M. Newton, pers. comm., Dec. 1984) but also by mammals feeding on the fruit.

Seed Viability and Germination: Seeds of thimbleberry are believed to remain viable for a long period of time, like those of other members of the *Rubus* genus. The species is considered to be a seed banker (M. Newton, pers. comm., Dec. 1984). Kellman (1969) found buried viable seeds of thimbleberry in a soil core taken from a mature conifer forest near Haney, B.C.

The seed has moderate viability in germination tests (maximum 62%), and requires approximately 90 days of chilling to germinate. Acid treatment may also promote germination (Marchant and Sherlock 1984). Germination of buried and newly deposited seed is believed to be the principal means by which thimbleberry invades new areas. Abundant seedlings are present on disturbed sites within the 1st year following disturbance (Kelpsas 1978; Stewart 1978; M. Newton, pers. comm., Dec. 1984).

Vegetative Reproduction: Thimbleberry is a strongly rhizomatous species (Stickney 1981; Marchant and Sherlock 1984), and once it is established on a site, further expansion of the colony is probably achieved through the spread of rhizomes. The species can be readily propagated in the spring through cuttings and fragments of rhizomes (Marchant and Sherlock 1984).

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[84] Brand, 1984.
[85] Ibid.

PREDATION AND PESTS

Thimbleberry fruit is a favoured food species of many birds and mammals. Gilbert (1980) describes some species of aphid (*Masonaphis* spp.) that occur widely on thimbleberry.

EFFECTS ON CROP TREES

Competition: Thimbleberry is a very important competitor with coniferous trees in B.C., particularly in the Prince Rupert and Prince George Forest Regions, where it may be the most widespread problem species (C. Delong, pers. comm., Nov. 1984; M. Geisler, pers. comm., Jan. 1985). It very rapidly and aggressively takes over clearcut areas, particularly on moist, productive ecosystems. On coastal alluvial sites in northwestern B.C., it causes greater and more rapid mortality of young conifer seedlings than any other brush species (J. Pollack, pers. comm., Jan. 1985).

Thimbleberry produces a dense canopy of large leaves that allows very little light to penetrate.[86] Exclusion of light seems to be its primary mode of competition with young seedlings, but the dense subterranean network of rhizomes and roots must also compete very effectively for moisture and nutrients. Thimbleberry annually produces large quantities of litter that can smother young seedlings (M. Newton, pers. comm., Dec. 1984). In a western Washington study, extracts of leaves and litter were found to inhibit growth of test plants in the laboratory, but there was no evidence that allelopathic effects were occurring in nature (del Moral and Cates 1971).

Thimbleberry will rarely invade a site already occupied by other species (M. Newton, pers. comm., Dec. 1984)

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Where thimbleberry is present on a site prior to logging it will rapidly increase in cover and vigour following canopy removal. It will also quickly invade unoccupied, cleared sites through germination of buried and recently deposited seed. In the SBS zone north of Prince George, thimbleberry increased to 40% cover on a Devil's club site type and to 15% cover on an Alluvium site type 6 years after clearcutting, but did not increase significantly on the drier site types (Eis 1981). On the Devil's club site type it was apparently able to take advantage of vacant growing space caused by die-back of devil's club while on the Alluvium site it faced stronger competition from other shrub species. In a study near Vancouver, thimbleberry increased in height from 1.0 to 2.0 m after canopy removal.[87]

Fire: Thimbleberry cover is significantly increased by fire (Lafferty 1972; Wright 1972; Stickney 1981). If present prior to burning, it will resprout vigorously from rhizomes and root crowns (Wright 1972). It also seeds in readily to unoccupied burned ground (Kelpsas 1978; Stewart 1978). On moist, productive ecosystems in the CWH zone near Vancouver, thimbleberry was abundant from the 1st year following burning and remained abundant for at least 5 years after a fire.[88]

Cutting: Manual cutting of thimbleberry is considered an ineffective means of control because cutting stimulates rapid resprouting[89] and increases total leaf area (Gratkowski 1978).

Herbicides: A wide variety of herbicides have been tested against thimbleberry in Oregon and Washington (Gratkowski 1971, 1978). Thimbleberry was judged moderately sensitive to most treatments but will usually resprout, necessitating respraying 1–2 years after treatment. In coastal B.C., and the northwestern U.S., late summer or fall applications of glyphosate have been very effective (Miller and Kidd 1983; Conard and Emmingham 1984*a*; J. Pollack, pers. comm., Jan. 1985). An aerial spray of 2.25 kg/ha in late July also provided excellent control after one growing season near Prince George (Expert Committee on Weeds 1984). However, thimbleberry appears to be quite resistant to hexazinone (Miller and Kidd 1983; Expert Committee on Weeds 1984), and triclopyr (Miller and Kidd 1983; Conard and Emmingham 1984*a*).

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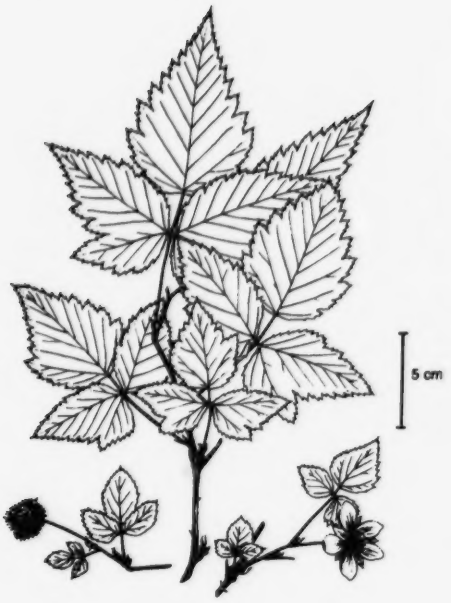
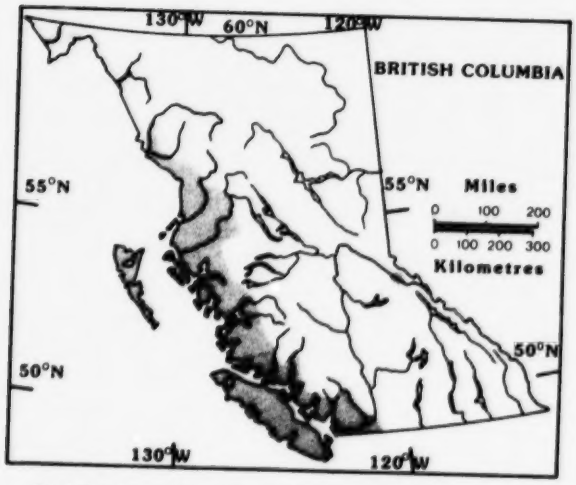
[86] Brand, 1984.
[87] Ibid.
[88] Ibid.
[89] Ibid.

Soil Disturbance: Thimbleberry quickly invades disturbed soils either by rhizomatous growth or through germination of seeds. In the CWH zone near Vancouver, thimbleberry rapidly increased in dominance and vigour following scarification of moist productive ecosystems.[90] Thimbleberry was the most vigorous plant invader of blade-scarified seedbeds on moist spruce-fir sites near Prince George (Arlidge 1967). Within 3 years of scarification it had totally occupied plots in the Devil's club site type and had reached a height of over 1 m.

[90] Brand, 1984.



Rubus spectabilis (salmonberry).



Distribution of *R. spectabilis* in British Columbia.

Rubus spectabilis Pursh. — Salmonberry

DESCRIPTION

Salmonberry is a thicket-forming deciduous shrub arising from a branching rhizome. The stems are erect or curved, 0.6–3 m tall. Twigs are hairless, with scattered spines or prickles, and grow in a zigzag manner. Salmonberry has compound leaves with three sharply toothed leaflets. The showy, deep pink flowers blossom early in spring and are followed by a glossy red to yellow "raspberry-like" aggregate fruit consisting of many small drupelets (Viereck and Little 1972; Taylor 1973*b*; Hultén 1974).

Variation: No subspecies or varieties of salmonberry are described in British Columbia (Taylor and MacBryde 1977), but it is reported to hybridize with *R. idaeus* and *R. arcticus* in Alaska (Viereck and Little 1972; Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Salmonberry occurs along the entire length of the coast of B.C. including Vancouver Island and the Queen Charlotte Islands. It is primarily found on the west side of the Coast Mountains, but penetrates inland along the Skeena and Fraser river drainages. It has been recorded from one location on the upper Fraser River (A. Češka, pers. comm., Dec. 1984), but is otherwise absent from the Interior Wet Belt. Salmonberry is very abundant in the CWH, CDF, and CCPH biogeoclimatic zones and occurs frequently in the MH zone.

Altitudinal Range: Salmonberry extends from sea level to lower alpine elevations (Hultén 1974), but is most abundant below approximately 800 m (Lyons 1952). At low elevations it is common in a variety of habitats, but at high elevations it tends to be restricted to streambanks and rarely develops extensive stands (Barber 1976).

HABITAT

Climatic Relations: Salmonberry clearly favours a humid to perhumid coastal climate with relatively mild temperatures and a lengthy growing season. It reaches its best development in B.C. at low elevations on the south Coast. At the northeast extent of its range in the Nass and Bulkley valleys it occurs only in sheltered, humid locations and is noticeably reduced in size and vigour.

Site and Soil Conditions: Throughout its range, salmonberry is a species of lowland forests, moist slopes, and stream banks (Ruth 1970; Viereck and Little 1972; Barber 1976; Campbell and Franklin 1979). It occurs on a wide range of soil textures and parent materials from rich loams to loamy clays, on rapidly drained gravels and on peat (Barber 1976), but best growth occurs on floodplains. Soils on which salmonberry is abundant include Brunisols, Regosols, Gleysols, Podzols, and Organics (see e.g., Klinka and Carter 1980; Yole *et al.*;[91] Banner *et al.*[92]).

Nutrient Relations: Salmonberry apparently favours sites with a medium to very rich nutrient status,[93] but Barber (1976) concluded that soil fertility is relatively unimportant for its growth and survival compared to other habitat factors. Salmonberry may have a fairly high demand for nitrogen (M. Newton, pers. comm., Dec. 1984). A soil nitrogen study by Barber (1976) indicates that salmonberry will survive and grow whether nitrogen is provided as ammonium or nitrates.

Water Relations: Salmonberry is a mesic species that reaches its best development where soil moisture is plentiful but not abundant. Best growth occurs when soils are well aerated and near field capacity. In wet, poorly aerated soils, root growth is inhibited; the plant declines in size and vigour and occurs mainly on elevated hummocks (Barber 1976). Salmonberry is apparently poorly adapted to survive under droughty conditions as a young seedling (Ruth 1970). On dry sites, it has a compact growth form; extensive shoot growth appears to be delayed, limiting transpirational losses until roots are sufficiently developed to assure a continuous supply of soil moisture (Barber 1976).

Light Relations: Salmonberry is described as shade-tolerant (Ruth 1970) or semi-tolerant.[94] Its ability to achieve net photosynthesis at low light levels permits it to inhabit sites too shady for other species of the *Rubus* genus (Barber 1976). Best growth occurs in forest openings and cleared areas where abundant

[91] Yole *et al.*, 1982.
[92] Banner *et al.*, 1983.
[93] Brand *et al.*, 1984.
[94] Ibid.

moisture is available (Ruth 1970; Campbell and Franklin 1979). In some situations, salmonberry seedlings appear to prefer partial shading, but moisture stresses rather than excessive radiation limit the survival and growth of seedlings in full sunlight (Ruth 1970). Salmonberry is virtually eliminated under dense coniferous canopies (Barber 1976).

The shade tolerance of salmonberry may be greater in the Pacific Northwest states and in south coastal B.C. than towards the northern limits of its range. Salmonberry is a dominant understory species under red alder and mixed alluvial forests in the southern half of its range, but it is uncommon as an understory species in southeastern Alaska (P. Alaback, pers. comm., Dec. 1984), and it frequently has low vigour under dense red alder on alluvial sites on the Skeena River (authors' personal observation).

Temperature Relations: Salmonberry is able to achieve net photosynthesis at relatively low temperatures. This adaptation may allow it to make maximum use of available solar energy by resuming activity much earlier in the growing season than associated and overtopping deciduous species (Barber 1976).

GROWTH AND DEVELOPMENT

Like other *Rubus* species, salmonberry is a perennial rhizomatous shrub with relatively short-lived above-ground stems or canes. Viereck and Little (1972) report that the canes are biennial, like those of raspberry, but this seems to be untrue, at least in some portions of the species' range. Healthy canes of at least 10 years of age, and possibly as old as 15 years have been found in southern B.C. (D. Bigley, pers. comm., Nov. 1984).

Salmonberry forms dense thickets of erect to prostrate stems. It is normally 1–3 m tall but can be as tall as 5 m (Hitchcock *et al.* 1969). Under favourable conditions, height growth can be as much as 1.5–2 m in a single growing season (Barber 1976).

The rhizomes spread laterally beneath the soil, producing new shoots at a distance of 1–2 m from the parent plant. Clonal colonies measuring several metres across develop in this manner. Pure stands of salmonberry which may have arisen from a single plant through vegetative reproduction can be more than 100 m across (Barber 1976).

Phenology: Salmonberry is described by Barber (1976) as a species with "precocious" phenology. Both above- and below-ground growth commence very early in the spring, before associated plants such as red alder and thimbleberry have become active. This precocious development is seen as an adaptive strategy giving salmonberry a competitive advantage as an understory species.

In western Washington and Oregon, leaf emergence can begin in March, even when snow is still present (Stewart 1974*b*; Barber 1976). Leaves flush during early April on the central B.C. coast, and are fully expanded by early May (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.). Flowering normally takes place between April and June on the south Coast of B.C,[95] and from April to July in southeastern Alaska (Viereck and Little 1972), but flowers have been recorded from southern Vancouver Island as early as late January during some mild winters (Clark 1976). Pojar (1975) notes that flowering in this species is correlated with the arrival of migrating Rufous Hummingbirds along the length of the Pacific coast. Fruiting begins early and can extend for a period of more than 2 months (Barber 1976). On the central B.C. coast, ripe fruits were present from early June to July (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.), while in Alaska the first fruits are ripe in early July at low elevations and in August at higher elevations (Viereck and Little 1972). Salmonberry does not set terminal buds at the end of the growing season; stem elongation can potentially continue as long as soil moisture is available and temperatures are favourable (Barber 1976).

REPRODUCTION

Seed Production and Dispersal: Salmonberry has a perfect, simple flower. Pollination is achieved primarily by insects and hummingbirds present during the early spring flowering period (Pojar 1975; Barber 1976). The fruit of salmonberry is an aggregate of small drupelets each containing a single hard-coated seed. Large quantities of seed are produced each year (Barber 1976). The fruit falls readily to the ground and most seed is probably deposited immediately below the parent plant. Wider dispersal is primarily by birds and mammals that consume the fruit.

[95] Brand, 1984.

Seed Viability and Germination: Seeds of many species of *Rubus* are known to have extended viability and may last for long as 100 years. Most researchers believe that storage of viable seed in the forest floor for long periods of time is an important aspect of the reproductive strategy of salmonberry (Ruth 1970; Barber 1976). Soil disturbance and increased sunlight apparently stimulate germination of the stored seed (Krygier and Ruth 1961).

Germination of salmonberry seed normally requires several months of chilling followed by warm temperatures. Passage through the crop or gut of a bird apparently scarifies the seed and enhances germination. Seeds germinated under laboratory conditions are usually treated with acid (USDA 1974; Barber 1976). Seeds from red and yellow fruit are equally viable (Barber 1976).

Seedlings of salmonberry are uncommon except where soil disturbance has occurred. Light is apparently not necessary for seed germination but is critical for subsequent seedling survival (Barber 1976). Seedlings will germinate on peat, decaying logs and stumps, and in a variety of habitats (Barber 1976), but mineral soil is apparently required for successful establishment (Ruth 1970).

Seed is very important in allowing salmonberry to invade new areas and in enabling the species to persist in environments where natural disturbances are infrequent. Seedling production is not significant in perpetuating established colonies (Barber 1976).

Vegetative Reproduction: Vegetative reproduction is the principal means by which expansion and perpetuation of established colonies of salmonberry takes place. Salmonberry is strongly rhizomatous and the lateral spread of rhizomes followed by production of new shoots is the primary mode of vegetative reproduction. Vigorous formation of adventitious shoots is usually stimulated by some form of disturbance (D. Bigley, pers. comm., Nov. 1984). Tip layering is another mode of asexual reproduction (Barber 1976). Where plants are fragmented by soil disturbance, rhizome and root fragments can be expected to reroot and produce new plants (Krygier and Ruth 1961).

PREDATION AND PESTS

Salmonberry is an important forage species for many coastal animals. The foliage is browsed by elk, deer, moose, and mountain goats (Viereck and Little 1972) while the berries are consumed by birds, coyotes, and bears (Viereck and Little 1972; Barber 1976).

Barber (1976) describes salmonberry as relatively free of insects and disease, and lists some of the more important pest species.

EFFECTS ON CROP TREES

Competition: Salmonberry is a major competitor of young conifers on moist, productive sites in most of coastal B.C. Dense thickets of salmonberry inhibit establishment of natural and planted conifers (Gratkowski 1971; Viereck and Little 1972; Campbell and Franklin 1979). Light intensities beneath a dense stand of salmonberry are too low to permit seedling establishment; mats of leaf litter may prevent germination or smother young seedlings. Other competitive factors are presumably also at play (Barber 1976). Although extracts of salmonberry leaves and litter inhibited growth of test plants in the laboratory, no allelopathic effects of salmonberry litter on conifer growth have been demonstrated under field conditions in western Washington (del Moral and Cates 1971).

Barber (1976) suggests that Douglas-fir may be more susceptible to salmonberry competition than species such as western hemlock with greater shade tolerance. However, in an experiment by Newton and White (1983), small hemlock seedlings sustained more damage from salmonberry than did Douglas-fir or Sitka spruce. Once it is overtopped by conifers, salmonberry is quickly at a competitive disadvantage. It can be shaded out by a dense 15- to 20-year-old hemlock overstory (Barber 1976).

Beneficial Effects: A dense colony of salmonberry can inhibit invasion of long-lived deciduous species such as red alder, bigleaf maple, and black cottonwood (Campbell and Franklin 1979). Salmonberry may also act to reduce soil erosion (Barber 1976).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Salmonberry often develops into dense thickets following timber harvest. On areas where salmonberry is present in the understory prior to logging, canopy removal results in a rapid increase in

colony size, crown cover, and stand density. Cover increased from 1.1 to 14.6% over a period of 7 years (Ruth 1970). Height growth of salmonberry may not increase significantly following canopy removal (D. Bigley, pers. comm., Nov. 1984).

Ruth (1970) also reported prolific germination of young salmonberry seedlings from seed stored in the duff following canopy removal and associated soil disturbance. The degree of canopy removal did not appear to affect the germination rate of seedlings, but some shade helped to prevent dessication of young seedlings.

Ruth predicted that successive thinnings in intensively managed stands will allow salmonberry to persist in the understory to a greater extent than was possible in undisturbed mature forests. This may lead to greater salmonberry competition problems in future rotations.

Fire: Salmonberry rapidly increases in cover following natural or prescribed fire. Broadcast burning retards brush for about one season but subsequent sprouting of salmonberry is dense (Krygier and Ruth 1961). Invasion of unoccupied ground takes place through spread of rhizomes and natural seeding (Allen 1969). Eighteen months following prescribed burning near Haney, B.C., salmonberry seedlings were abundant (D. Bigley, pers. comm., Nov. 1984). A study in the CWH zone near Vancouver found that salmonberry increased significantly following logging and burning and was abundant within 3 to 4 years of harvest,[96] but the results do not indicate whether burning itself enhanced salmonberry cover. Morris (1970) found that salmonberry cover was higher on unburned clearcuts than on burned sites during the first five growing seasons in Washington and Oregon, however, by the 11th to 16th growing seasons, there was no difference in relative abundance of salmonberry on burned and unburned sites. Effective control of salmonberry can be achieved with an intense burn that consumes the litter, destroying stored seed and underground organs; however, such a burn can cause significant site degradation (M. Newton, pers. comm., Dec. 1984).

Cutting: Manual cutting of salmonberry stimulates rapid resprouting from stem bases and rhizomes, and can result in an increase in total leaf area (Brand;[97] M. Newton, pers. comm., Dec. 1984). Salmonberry cut to ground level in May near Vancouver had regrown to over 1 m in height by August of the same year (D. Bigley, pers. comm., Nov. 1984)

Herbicides: Before glyphosate became available for forestry use, salmonberry was very difficult to control with herbicides as subterranean parts were frequently unnaffected, and the plant tended to resprout from rhizomes and stem bases (Stewart 1977).

Late summer and fall application of glyphosate cause severe mortality of salmonberry in western Washington and Oregon, while 2,4-D causes only light to moderate damage (Conard and Emmingham 1984*a*; S. Conard, pers. comm., March 1985). Mechanically damaged salmonberry stems can be more resistant to glyphosate than undamaged stems (Kelpsas 1978).

Soil Disturbance: Soil disturbance that exposes mineral soil provides a suitable seedbed for salmonberry germination and may stimulate germination of buried seed. Damage caused to existing salmonberry plants will stimulate resprouting, and fragments may reroot to produce new plants (Krygier and Ruth 1961; Ruth 1970; Barber 1976). Scarification of clearcut areas in the CWH zone near Vancouver resulted in a rapid increase in salmonberry cover over prelogging conditions.[98] Deep scarification can reduce salmonberry cover if roots and rhizomes are completely removed from the soil (M. Newton, pers. comm., Dec. 1984).

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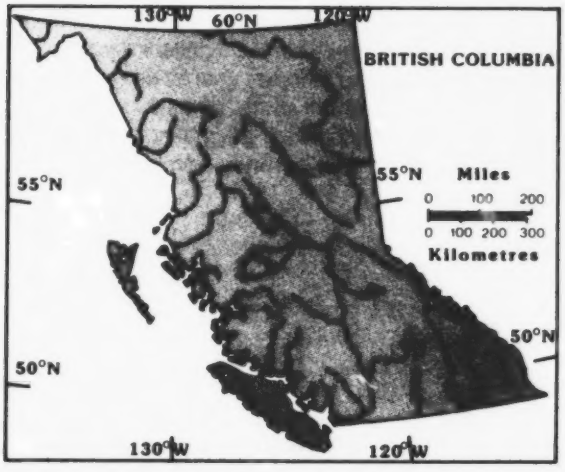
[96] Brand, 1984.
[97] Ibid.
[98] Ibid.

Salix bebbiana (Bebb's willow).



Distribution of willows (*Salix* spp.) in British Columbia.

Salix spp. L. — Willows

DESCRIPTION

The willows are a highly variable group of small trees, shrubs, and creeping woody plants. Form and leaf characteristics vary widely but all willows have single-scaled buds and lack a terminal bud. Leaves are linear or lanceolate to orbicular but usually narrow and without large teeth. Male and female flowers are borne in catkins on separate plants. The fruit is a capsule that splits into two valves to release many downy seeds (Argus 1973; Brayshaw 1978).

Variation: Salix is an extremely variable genus with extensive hybridization between species, although probably more hybrids have been described than exist in nature because of the high degree of intraspecific variation (Argus 1973; Brayshaw 1978). There are 48 species of willow in British Columbia (Taylor and MacBryde 1977), but only a small percentage are important in a silvicultural context.

DISTRIBUTION AND ABUNDANCE

Willows occur throughout B.C. The following table lists some of the most important willows on forested sites and describes their distribution and habitat (after Brayshaw 1978; Roberts[99]; J. Pojar, pers. comm., Oct. 1984):

Species	Distribution	Habitat
S. sitchensis	Common on the Coast and scattered inland	River bars and uplands
S. scouleriana	Throughout B.C.; the most common coastal sp.	Uplands and moist draws
S. bebbiana	East of Coast Mtns.; the most common Interior sp.	Uplands and disturbed sites
S. glauca	East of Coast Mtns.	Uplands and wetlands, low and high elevations
S. hookeriana	Along Coast; very common in Fraser Valley	Swamp edges
S. lasiandra	Throughout B.C.	Alluvial habitats
S. pyrifolia	Northeastern B.C.; abundant in Peace R. area	Wetland margins, riparian habitats
S. barclayi	Throughout B.C. at higher elev. and in northern areas	Variable
S. arbusculoides	Boreal forest and central Interior	Upland forest and wetlands
S. planifolia	Low to moderate elevations, mostly boreal forest forest	Wetland margins
S. maccalliana	Widely scattered; abundant in Chilcotin	Wetland margins
S. rigida	Throughout B.C., especially in southern Interior	Mostly in bottomland
S. drummondiana	East of Coast Mtns.	Alluvium and wetlands
S. alaxensis	Northern B.C.	Open, rocky soils and river bars

Altitudinal Range: Willows occur at all elevations in B.C., from sea level to alpine (Lyons 1952; Brayshaw 1978).

HABITAT

Climatic Relations: Willows grow throughout the world, but are best adapted to a cool, moist northern climate (Brayshaw 1978). The species in B.C. are adapted to all extremes of climate found in this province. In temperate and warmer climates, willows are often most prevalent in locations with a cool microclimate.

[99] A. Roberts. 1983. A guide to the willows of the Cariboo Forest Region. B.C. Min. For. Williams Lake, B.C. Unpublished report.

Site and Soil Conditions: Best willow growth occurs in deep, moist, alluvial bottomlands (Rawson 1974), but there are willows on every imaginable type of site and soil. Most willow species are adapted to moist-to-wet riparian or swamp habitats with gleyed, regosolic or organic soils, but some of the most abundant species favour well-drained sandy or gravelly parent materials (Rawson 1974; Brayshaw 1978).

Nutrient Relations: The general pH range for willows is 5.5 to 7.5. They will tolerate moderately alkaline soils, but apparently do poorly on extremely alkaline or acidic soils (Rawson 1974). The genus contains species adapted to a wide variety of nutrient conditions, but the greatest diversity of forest species is found on favourable, nutrient-rich habitats. In the SBS zone, Bebb's willow (one of the most common upland willows) is found mainly on medium to nutrient-rich forest sites (Pojar *et al.* 1982).

Water Relations: Although willow species are adapted to the full range of soil moisture conditions in most forest zones in B.C., the majority are found on moist, subhygric and wetter sites. Many species will tolerate standing water (Brayshaw 1978), but growth can be severely reduced when water levels are maintained at or above the root collar for extended periods (Knighton 1981). Willows growing along waterways in arid areas are described as "water-wasting" by Kozlowski (1972) because they transpire large quantities of water.

Light Relations: Willows are moderately to highly shade-intolerant. Most species grow in the open or in partial shade, and vigour is much reduced under a forest canopy (Lyons 1952; Rawson 1974).

Temperature Relations: The ability of some willows to grow in the most extreme northern and alpine environments (Argus 1973; Brayshaw 1978) attests to their tolerance of extreme cold.

GROWTH AND DEVELOPMENT

Willows range in size from medium-sized trees to dwarf shrubs, but most species of significance on forested sites are tall or medium-sized shrubs, or small trees no more than 10 m in height. They generally have a broad crown and are frequently multistemmed. Many species form dense thickets on wet sites (Rawson 1974; Brayshaw 1978), but upland willows often occur as scattered individuals. A remarkable characteristic of willows is their plasticity (Brayshaw 1978); the growth form adapts readily to habitat conditions, and there is extreme variability in branching habit, and foliage characteristics.

Willows exhibit rapid early growth from both seed or sprout (Rawson 1974). Sprout growth far exceeds that of seedlings and can exceed 2 m in 1 year (G. MacKinnon, pers. comm., Jan. 1985). Most willows are short-lived and become decadent at an early age (Spector 1956, cited by Rawson 1974; Fowells (compiler) 1965).

Phenology: A distinctive characteristic of some willows is the production of "pussy willows" early in spring before the snow has melted (Viereck and Little 1972). The genus typically has an early flowering phenology. Many species flower well before the leaves have emerged, others flower simultaneously with leaf emergence, while still others flower late in the year after the leaves have fully expanded. Seed ripening closely follows flower development, and most species disperse seed in early or midsummer (Zasada and Viereck 1975; Brayshaw 1978; Marchant and Sherlock 1984).

REPRODUCTION

Seed Production and Dispersal: Willows are early producers, and begin to flower at between 2 and 10 years of age (USDA 1974). Male and female flowers occur on separate plants, so many plants never produce seed. Bees are apparently important in pollination. The optimum seed-bearing years of Bebb's willow are 10–30 years (Rawson 1974). In an Alaska study, a 2-year-old sprout produced seeds (Zasada *et al.* 1983). Most willows produce prolific quantities of seed (Brayshaw 1978). The capsular fruits split to release the minute, downy seeds that are then dispersed by either wind or water (USDA 1974).

Seed Viability and Germination: Willow seed has an extremely short period of viability. Under natural conditions, most seeds remain viable for only a few days. Seeds usually germinate within 12–24 hours of landing on a suitable seedbed (USDA 1974). In artificially sown seedbeds in Alaska, viable seeds were found after 4 weeks, but most germination occurred within 2 weeks of seeding (Zasada *et al.* 1983). In germination tests, willows normally have a high germinative capacity (70–100%) (USDA 1974; Zasada *et al.* 1983). Seed dormancy is absent in most species (USDA 1974; Marchant and Sherlock 1984), but has been observed in some late-flowering Alaskan species whose seed germinates in the spring of the following year (Zasada and Viereck 1975; Holloway and Zasada 1979). Germination is best under moist conditions with high relative

humidity and full sunlight (USDA 1974). Exposed mineral soil is the best seedbed for many willow species, and germination of the small seed is inhibited on sites with a continuous cover of tree litter (Grime 1979).

Vegetative Reproduction: Willows are well known for their ability to root readily from stem cuttings (Edlin 1966; Marchant and Sherlock 1984). Cuttings taken during the growing season root particularly well (Holloway and Zasada 1979). Rooting is usually most successful on moist to wet sites (Rawson 1974; G. MacKinnon, pers. comm., Jan. 1985). Stem and root fragments root naturally if buried in moist soil. Damaged and cut stems produce prolific sprouts from the stem base or root collar (Fowells (compiler) 1965; Rawson 1974). Layering also occurs readily if branches are buried (Marchant and Sherlock 1984). The sandbar willow (*S. interior*) reportedly expands by developing suckers from its extensive root system (Neiland and Viereck 1977).

PREDATION AND PESTS

Willows are the staple food of moose (Murie 1954), and are a prime source of summer and winter food for deer (Aldous 1952). Willow shoots, buds, and catkins are eaten by many rodents, small mammals, and birds (Rawson 1974).

Furniss and Krebill (1972) recorded 52 species of insects and 39 species of fungi that attack willows in the western U.S.

EFFECTS ON CROP TREES

Competition: Willows compete with coniferous crop trees on a variety of sites throughout B.C. Willow competition is widespread throughout the Interior, but is most intense in the northern SBS and in the BWBS where willows are extremely abundant and have become dominant over extensive areas as a result of repeated fire. On the Coast, willow competition is significant primarily in wet or alluvial habitats.

Rapid early growth, especially in plants of sprout origin, allows willow to quickly outgrow its competitors (Rawson 1974). The plant can expand very rapidly following disturbance (Mueggler 1965), and its tendency to form dense thickets inhibits natural regeneration of conifers. The canopy of mature trees seldom creates deep shade, but juvenile growth may have larger leaves and dense sprouts can produce a solid canopy.

Beneficial Effects: No direct beneficial effects of willow on conifer growth are reported in the literature. Willows are useful in stabilizing streambanks and provide erosion control on severely disturbed sites (USDA 1974; Marchant and Sherlock 1984).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Willow generally increases in abundance on cutover areas (Mueggler 1965; Viereck and Little 1972; Eis 1981), but invasion is not always rapid. Trees damaged or cut during harvesting operations will sprout vigorously. Increased sunlight following overstory removal is very favourable to willow. Mueggler (1965) found that crown cover of willow was 10 times greater on areas with low overstory cover than under a closed forest canopy.

Fire: Willow is greatly favoured by fire in most habitats (Wright 1972). It can become the dominant cover in areas that have a history of frequent natural fire. In northern Idaho, cover of *S. scouleriana* was dramatically higher on sites that had been burned, particularly where there had been repeated fires over a 30-year period (Mueggler 1965). Four years following a fire in Alaska, *S. scouleriana* density was 4 times greater than on adjacent unburned areas (Viereck and Dyrness 1979). Stickney (1981) found abundant seedlings of this willow on burned sites in western Montana. He noted, however, that its rate of cover development from the seedling stage was quite slow; after 6 to 9 years its cover was less than 10% on most areas.

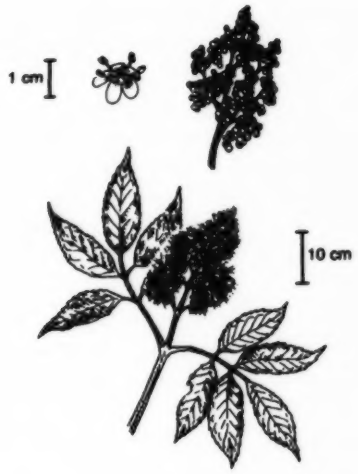
Prescribed fire is widely used as a wildlife management tool to rejuvenate decadent willow and stimulate sprouting. A quick, hot fire maximizes sprouting, while slower, longer burns cause more extensive damage and produce less browse (G. MacKinnon, pers. comm., Jan. 1985). However, in some situations prescribed burning can reduce initial competition from willow in clearcut areas (C. Delong, W.R. Mitchell, and D. Lloyd, pers. comm., Nov. 1984).

Cutting: Willow will sprout vigourously following cutting, regardless of cutting season. Sprouting vigour is more pronounced if cutting takes place during the dormant season. It is possible for individual cut stems to produce 50 or 60 sprouts, but sprout number is quite variable. Heavy clipping of willow in the northeastern

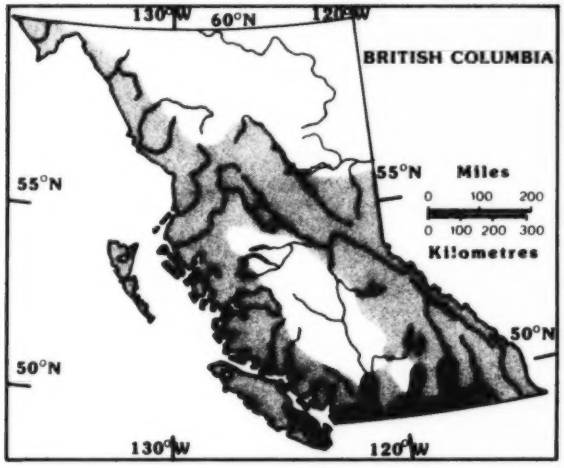
U.S. produced a major increase in twig production (Aldous 1952). Over 5 years of cutting, annual production increased steadily to 855% of initial production. Stem number was gradually reduced but individual stems were stouter and had greater vigour.

Herbicides: Herbicide response in willows is difficult to monitor because of the difficulty of identifying willow species. Because of the great variability both between and within species, herbicide response can vary dramatically (M. Newton, pers. comm., Dec. 1984). At a site near Dawson Creek, B.C., an aerial application of glyphosate at 3.0 kg/ha to Bebb's willow resulted in 70% defoliation after the first growing season, but few coppice stools were completely killed (Expert Committee on Weeds 1984). Conard and Emmingham (1984*b*) report that glyphosate applied in the late summer or fall causes very severe injury (90–100%) to willow in Oregon and Washington.

Soil Disturbance: Exposure of mineral soil favours the germination of willow seed (Grime 1979; Zasada *et al.* 1983). Along streambanks, willows are among the first species to seed-in to newly exposed silt and gravel (Neiland and Viereck 1977). Windrowing is used to increase willow browse production because mechanical damage to stems stimulates prolific sprouting. In addition, branch parts incorporated into the mineral soil during mechanical treatments have the potential to root and subsequently regenerate new plants (G. MacKinnon, pers. comm., Jan 1985).



Sambucus racemosa (red elderberry).



Distribution of elderberries (*Sambucus* spp.) in British Columbia. The shaded area represents the distribution of *S. racemosa*, while the hatched area shows the distribution of *S. cerulea*.

Sambucus spp. L. — Elderberry (Elder)

DESCRIPTION

Elderberry is a tall, coarse shrub or small tree with a broad, arching crown, 1–6 m tall. Branches are stout with a soft, pithy centre and large buds. Elderberry leaves are large and compound with five to eleven pointed, finely toothed leaflets. The flowers are small and white, borne in large, showy terminal clusters. The berry-like fruit can be bluish, purplish black, or brilliant red (Viereck and Little 1972; Hosie 1973; Clark 1976).

Variation: The taxonomy of the genus *Sambucus* in British Columbia is confusing because of the profusion of synonyms for each taxon. To the non-botanist there are three types of elderberry in B.C.: a blue elderberry, a red elderberry, and a black elderberry; to the plant taxonomist it is not quite so simple.

There are two species of *Sambucus* in B.C., one of which has several varieties. *Sambucus cerulea* is the large tree-like blue elderberry found only in southern B.C. The other species, *S. racemosa,* occurs through most of the province (Taylor and MacBryde 1977).

Sambucus racemosa is found across the Northern Hemisphere. Its North American version is now known as ssp. *pubens.* It can have either red or black fruit. In B.C., the black-fruited variety (var. *melanocarpa*) is found only in the southern Interior. There are two varieties with red fruit in B.C. Variety *leucocarpa* occurs virtually across Canada but is only found in southeastern B.C. Variety *arborescens* is found along the Pacific coast and through most of B.C. To complicate the issue, there is a third red-fruited variety (var. *microbotrys*) found south of the border in the U.S. Rocky Mountains. Most of the ecological literature available refers to this southern variety.

DISTRIBUTION AND ABUNDANCE

The table below summarizes the taxonomy and distribution of *Sambucus* in B.C. As much as possible in the remainder of this discussion, only the names of the two species, *S. cerulea* (blue fruit) and *S. racemosa* (either red or black fruit), will be used.

Scientific name *(synonym)*	Common name	Distribution in British Columbia
Sambucus cerulea *(S. glauca)*	blue elderberry	Southern B.C. and Vancouver Island; ICH, IDF, PPBG, CDF, and southern CWH
Sambucus racemosa* ssp. *pubens *(S. racemosa, S. pubens)*		
(a) *S. racemosa* ssp. *pubens* var. *melanocarpa (S. melanocarpa)*	black elderberry	Southeastern B.C. only; ICH, IDF, ESSF
(b) *S. racemosa* ssp. *pubens* var. *leucocarpa (S. pubens* var. *leucocarpa)*	red elderberry (eastern)	Southeastern B.C. only; ICH, ESSF
(c) *S. racemosa* ssp. *pubens* var. *arborescens (S. callicarpa)*	red elderberry (coastal)	Coastal and moist Interior areas, except southeastern B.C.; CWH, CDF, CCPH, ICH, MH, ESSF, SBS

Altitudinal Range: Elderberry is found mostly at low to moderate elevations within its range. *Sambucus racemosa* is most abundant below approximately 600 m on the Coast and 1200 m in the Interior (Lyons 1952).

HABITAT

Climatic Relations: *Sambucus cerulea* is confined to the southern-most valley bottoms in B.C. and apparently requires a warm, fairly dry climate with as long a growing season as is available in B.C. *Sambucus racemosa* appears to tolerate a broader range of climates and more severe conditions, but is restricted to areas of coastal or humid continental climate. In the U.S. Rocky Mountains, *S. racemosa* is found in moist, subalpine

climates where most of the precipitation falls as snow and temperatures during the growing season range from 5 to 25°C (Conrad and McDonough 1972).

Site and Soil Conditions: Elderberry is common along streams, ravines, and disturbed sites, and in forest openings on a wide variety of soils (UBC Bot. Garden 1971; Conrad and McDonough 1972; Viereck and Little 1972; Hosie 1973). *Sambucus cerulea* is most common on gravelly or stony soils (Hosie 1973), while *S. racemosa* generally occurs on deep, well-drained soils with silt loam to sandy loam textures (Harcombe *et al.* 1983). Best growth is on deep, fluvial soils.

Nutrient Relations: Elderberry favours rich soils (Clark 1976) and can be considered an indicator of high nitrate availability.[100] Ecosystem associations with *S. racemosa* as a common understory species are most often classified as moderately rich to very rich in nutrients (see e.g., Haeussler *et al.* 1984; Yole *et al.*[101]), but the species may be found under a broader range of nutrient conditions in seral ecosystems.

Water Relations: Throughout their ranges, the elderberries favour moist soil conditions (UBC Bot. Garden 1971; Viereck and Little 1972; Clark 1976). In areas of relatively dry climate such as the IDF zone, *S. racemosa* is restricted to subhygric and hygric sites where some moisture is available in addition to precipitation inputs. In wetter zones such as the ICH and CWH it can tolerate a broader range of moisture conditions (Angove and Bancroft 1983). *Sambucus racemosa* is common on some swampy skunk cabbage sites on the Coast,[102] but on these poorly drained sites it tends to occur on elevated hummocks.

Light Relations: *Sambucus cerulea* is described as slightly shade-tolerant by Plummer *et al.* (1955). *Sambucus racemosa* is tolerant of deep shade, but grows best in forest openings and margins (Harcombe *et al.* 1983). In a growth chamber experiment, *S. racemosa* grew better under 18-hour photoperiods than under 12-hour photoperiods (Conrad and McDonough 1972).

Temperature Relations: Best growth of *S. racemosa* in the growth chamber was under a 25°C daytime and 15°C nighttime temperature regime (Conrad and McDonough 1972). Seedlings kept at 2°C for 4 months to simulate winter conditions grew better than those that did not receive a chilling treatment. Branches are highly susceptible to killing by frost after growth has begun in spring.

GROWTH AND DEVELOPMENT

Seedlings of *S. cerulea* have a thick taproot and expansively spreading lateral root systems (Landis and Simonich 1984; Shaw 1984). Once established, the shrub grows rapidly in height and produces a large, full crown. Shrubs can attain their full size of approximately 3 m in height and several metres in crown diameter within 3 to 4 years in the Intermountain U.S. (Plummer *et al.* 1955). Most individuals remain as large shrubs but in favourable locations they can become small trees. Trees of advanced age can be 9 m tall and have diameters of 36 cm (Hosie 1973; Clark 1976).

The growth and development of *S. racemosa* var. *microbotrys* have been studied in the U.S. Rocky Mountains where it forms pure dense stands in subalpine rangelands (McDonough and Tew 1967; Conrad and McDonough 1972). In this environment red elderberry has a rhizomatous habit and spreads to form clones ranging in size from 1 to 16 m^2. The variation in clone size is believed to reflect age differences. Once established, a single clone can occupy the same site for a long period of time. One rhizome was found to be 58 years old and the age of the clone was probably much greater. Roots extend to a depth of approximately 1 m in the soil and there is a dense network of rhizomes and roots under the entire area of the clone.

In a greenhouse study it took 3 years before a red elderberry seedling was able to produce rhizomes. The rhizomes form buds that give rise to aerial stems. The stems of elderberry are canelike, with a soft pithy centre. During the first growing season these stems are unbranched and strictly vegetative. Axillary buds formed late in the growing season can develop into either vegetative or flowering branches the following year. Some axillary buds near the base of the stem remain dormant until branches higher on the stem are damaged. The erect stem produces secondary and then tertiary branches, but branches of tertiary or higher order are frequently killed by winter damage, so the branching habit of the plant remains quite simple. If stems are damaged or destroyed right

[100] Brand, 1984.
[101] Yole *et al.*, 1982.
[102] Ibid.

to ground level, new stems will emerge from dormant buds on the rhizome. Aerial stems newly arising from rhizomes have a much higher growth rate than branches on older stems.

Total above-ground biomass production at a site in Utah averaged 1000 kg/ha per year, equally divided between stem and leaf tissue (Conrad and McDonough 1972).

There are no reports of rhizomatous suckering activity in *S. racemosa* growing on the Coast (i.e., var. *arborescens*) (M. Newton, pers. comm., Dec. 1984). On the Pacific Coast, seedlings can grow 30 cm in the 1st year (M. Newton, pers. comm., Dec. 1984), and young shrubs can grow 1.3–2 m in a single year once established (UBC Bot. Garden 1971). Following any form of disturbance the species sprouts vigorously from the rootstock. Sprouts have considerably more rapid growth rates than seedlings and average 3–4 m in the 1st year (M. Newton, pers. comm., Dec. 1984). Red elderberry sprouts are possibly the fastest growing shrub in the Pacific Northwest.

Phenology: Growth of *S. racemosa* begins very early in the growing season. In the Rocky Mountains of the U.S., bud elongation begins while snow is still on the ground and stem growth is completed within 3 to 6 weeks following snowmelt (Conrad and McDonough 1972). On the central B.C. coast, most shrubs are in full leaf by mid June (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.).

Red elderberry blooms throughout May in southern B.C. (Lyons 1952) and from May to July in Alaska (Viereck and Little 1972). In the U.S. Rocky Mountains initiation of flower buds for the following year coincides with a sharp reduction in the rate of vegetative growth during late June and early July. Vegetative branches continue to elongate long after flowering branches have ceased to grow (Conrad and McDonough 1972). Berries become ripe in June in southern B.C. (Lyons 1952) and on the central Coast (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.), and during July and August in Alaska and the Rocky Mountains (Conrad and McDonough 1972; Viereck and Little 1972).

Phenological observations of *S. cerulea* were made over a period of 9 years in the northern U.S. Rocky Mountains (Schmidt and Lotan 1980). Bud burst occurred from late April to mid-June, depending on location and weather conditions. Where it occurs together with *S. racemosa* it usually leafs out about a month later than the red-fruited shrub (Clark 1976). Leaves were fully grown approximately 1 month after bud burst. Leaf senescence began in mid- to late August and leaf fall took place between mid-September and mid-October. Flowering of this species extends from late May through to August, and fruits ripen in August and September both in the U.S. and B.C. (Lyons 1952; Schmidt and Lotan 1980).

REPRODUCTION

Seed Production and Dispersal: Approximately 60–90% of the flowers in an inflorescence develop a small, round fruit containing two to five seed-like stones (Conrad and McDonough 1972; Hitchcock and Cronquist 1973). Good seed crops are produced virtually every year. Seed dispersal is primarily by birds and other animals that eat the fruit.

Seed Viability and Germination: Approximately 40% of seeds sampled by Conrad and McDonough (1972) were unfilled and only 50% of filled seed were viable. Seeds remain viable in storage for several years (at least 16 for *S. cerulea*). Seeds have both seed coat and embryo dormancy, and need several months of chilling before they will germinate. Additions of giberellic acid can increase germination rates. Germination of *S. racemosa* did not take place at 2°C but some germination occurred at 13°C (McDonough 1969; UBC Bot. Garden 1971; USDA 1974; Landis and Simonich 1984; Shaw 1984).

Germination of *S. racemosa* in a field experiment was only 1–8% (Conrad and McDonough 1972). The low germination may have been caused by freezing of the seed before a protective snow cover developed. None of the seedlings survived the summer. Few established seedlings were observed on undisturbed sites where *S. racemosa* clones were well established, and the authors concluded that production of seedlings is not a significant means of perpetuating established colonies. In contrast, germinants are often abundant on disturbed sites (Stewart 1978; M. Newton, pers. comm., Dec. 1984). Kelpsas (1978) found great quantities of germinants the first growing season following disturbance in coastal Oregon. The species was able to germinate on broken decaying wood.

Vegetative Reproduction: Elderberries reproduce vegetatively from sprouts, rhizome suckers, and by layering (Worley and Nixon 1974), although, as mentioned earlier, no suckering has been observed in coastal

Oregon. Vegetative reproduction is responsible for persistence of established colonies (Conrad and McDonough 1972).

PREDATION AND PESTS

Elderberry is highly palatable to livestock and many wildlife species including moose, deer, elk, and porcupine, who nibble on the buds and bark. The fruits are relished by many species of birds and small mammals (Plummer *et al.* 1955; UBC Bot. Garden 1971; Conrad and McDonough 1972; Worley and Nixon 1974; Harcombe *et al.* 1983).

The UBC Botanical Garden (1971) provides a list of insects and diseases found on *S. racemosa* ssp. *pubens* var. *arborescens* in B.C.

EFFECTS ON CROP TREES

Competition: Elderberry is a common shrub in moist, productive ecosystems in many areas of B.C. It is an important component of the complex of shrub species that can inhibit conifer regeneration and growth on such sites, but it is rarely a primary competitor. The shrub usually occurs as isolated clumps that spread over lower brush species. It easily outgrows conifers, particularly when it is of sprout origin.

Extracts of live plant material and litter of *S. racemosa* strongly inhibit germination and growth of Douglas-fir and grasses in the laboratory (McDonough and Tew 1967; del Moral and Cates 1971); however, these authors were unable to demonstrate that allelopathy is operative under field conditions.

Beneficial Effects: The presence of an overstory canopy of *S. cerulea* can aid in the establishment of other understory species in the relatively dry, hot climate of Idaho (Monsen 1984). Elderberry may also be helpful in erosion control on moist sites (Worley and Nixon 1974).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Harcombe *et al.* (1983) indicate that canopy removal will enhance cover of *S. racemosa*. Cover and frequency of *S. racemosa* was not significantly greater following logging in northern Idaho, but the height of the shrub increased (Mueggler 1965). Increases in total height and bushiness of red elderberry have also been observed following logging in the Cariboo Forest Region (R. Coupé, pers. comm., Nov. 1984). A definite increase in cover of *S. racemosa* was recorded 6 years following canopy removal on four site types in the SBS zone north of Prince George (Eis 1981).

Fire: There is conflicting evidence regarding the response of elderberry to fire. Several reports indicate that elderberry is favoured but not greatly enhanced by fire (Mueggler 1965; Lafferty 1972; Wright 1972). Seedlings are reported to be common on Coastal sites following fire (Stewart 1978) and existing plants respond to fire by sprouting from rootstocks (M. Newton, pers. comm., Dec. 1984). However, Brand did not record an increase in cover following burning in the CWH zone near Vancouver;[103] *S. racemosa* was only present in relatively undisturbed patches. Isaac (1940) reported that *S. cerulea* is quickly eliminated by fire because it spreads slowly by seed rather than rapidly by vegetative means.

Cutting: Red elderberry resprouts rapidly from stems and branches following cutting, but the plant cannot withstand repeated heavy clipping or browsing, especially when young (Aldous 1952; Harcombe *et al.* 1983). Conrad and McDonough (1972) conducted clipping experiments on *S. racemosa* var. *microbotrys* to simulate browsing by livestock. They found that cutting to ground level stimulated emergence of shoots from dormant rhizome buds within 2 to 4 weeks. Clipping in mid-June produced regrowth of 136% by the end of August. A second, late August clipping significantly reduced growth in the following year. Clipping once at the end of each growing season did not reduce the potential for regrowth. Clipping only lateral branches caused sprouting from buds at the base of the stem, whereas clipping back the entire stem caused new rhizome stems to emerge.

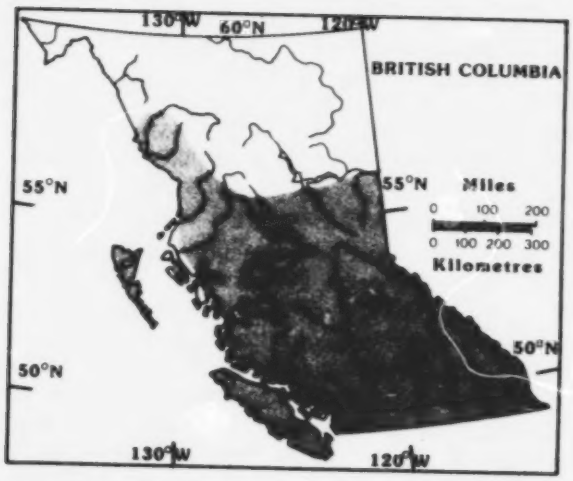
Herbicides: In northeastern Oregon and northern Idaho, spring applications of triclopyr with 2,4-D and fall applications of glyphosate both cause very severe injury (90–100%) to elderberry (Conard and Emmingham 1983). In western Washington and Oregon, spring applications of triclopyr and late summer

[103] Brand, 1984.

applications of glyphosate also cause very severe damage, but fall applications of glyphosate cause only 60–90% injury (Conard and Emmingham 1984a). One growing season after glyphosate was applied as a foliar spray at a rate of 2.25 kg/ha to red elderberry near Prince George, there was a 57% reduction in height but no reduction in percent cover, and rapid resprouting had taken place (Expert Committee on Weeds 1984). Elderberry was heavily damaged following a late August foliar application of 2 kg a.i./ha glyphosate in the Prince Rupert Forest Region (J. Pollack, pers. comm., Feb. 1985).

Soil Disturbance: Soil disturbance can create favourable conditions for germination of elderberry seedlings (Kelpsas 1978; Harcombe *et al.* 1983). Any soil disturbance that causes damage to stems and rhizomes will tend to stimulate vigorous resprouting from stem bases and possibly rhizome buds (Conrad and McDonough 1972; Worley and Nixon 1974; M. Newton, pers. comm., Dec. 1984).

Symphoricarpos albus (snowberry).



Distribution of *S. albus* in British Columbia.

Symphoricarpos albus (L.) Blake — Snowberry

DESCRIPTION

Snowberry is an erect, deciduous, small to medium-sized shrub (0.5–2 m tall) with a rhizomatous growth habit. Its twigs are slender with distinctly opposite branching. The thin leaves are exceedingly variable in shape, but most are ovate to elliptic with an untoothed margin. The flowers are tiny pink bells borne in small clusters. The fruit are clustered white drupes, remaining on the twigs over winter (Jones 1940; Viereck and Little 1972).

Variation: *Symphoricarpos* is a complex genus found throughout North America. The western species, *S. albus*, has two recognized varieties in British Columbia. The typical form, var. *albus*, is found east of the Coast range. The Coastal form, var. *laevigatus*, is larger and is sometimes regarded as a distinct species (Jones 1940; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Symphoricarpos albus is found throughout B.C. to approximately 56° N latitude. It has been found at scattered locations further north in the Stikine-Iskut drainage and on the Liard River, but is mostly absent from northern B.C. Snowberry is found along the coast including Vancouver Island and the Queen Charlotte Islands but occurs mostly slightly inland and is uncommon in the CCPH zone. It is most abundant in the IDF zone of southern B.C.

Altitudinal Range: Snowberry is a species of low elevations and is rarely found at subalpine elevations. It is usually limited to elevations below approximately 600 m on the Coast and 900 m inland (Lyons 1952).

HABITAT

Climatic Relations: Within its broad range in B.C., snowberry seems to favour areas of warm meso- or microclimate, and it is most abundant in some of the warmest, driest climates in the province. By contrast, in Colorado, towards the southern end of its range, snowberry favours moister, high elevations but is absent on dry south and west-facing slopes (Moore *et al.* 1975, cited by Watson *et al.* 1980). The coastal variety is apparently tolerant of humid — but not excessively rainy — conditions, while the Interior variety favours subhumid to semi-arid conditions. Neither variety seems able to tolerate the heavy snows and short growing seasons of high altitudes.

Sites and Soil Conditions: Snowberry has a broad ecological amplitude and can be found on a variety of sites and soils provided that climatic conditions are suitable. In the Interior it grows in rocky or dry soil, on river banks, in dry open rocky woods, and often at the base of cliffs (Jones 1940). It is often found on disturbed, coarse-textured and rocky soils in Alberta (Watson *et al.* 1980). On the Coast, snowberry is found on a variety of soils and parent materials supporting seral vegetation, and is often abundant on floodplains (see e.g., Harcombe *et al.* 1983; Haeussler *et al.* 1984).

Nutrient Relations: Snowberry is tolerant of mildly acidic to moderately alkaline conditions. It is somewhat tolerant of salts and will survive under low nutrient conditions (Watson *et al.* 1980). In the SBS zone, snowberry is described as occurring on sites that are medium to rich in nutrients (Pojar *et al.* 1982), but in other areas of the province it is found on ecosystems with a broad range of ecological nutrient regimes (see e.g., Mitchell and Green 1981; Utzig *et al.*[104]).

Water Relations: Snowberry has a broad ecological amplitude with respect to soil moisture (see e.g., Pojar *et al.* 1982). It can be found on very xeric sites and it is also abundant on subhygric and hygric sites. Although it tends to favour moist sites in dry subzones of the IDF and drier sites in wetter subzones (Angove and Bancroft 1983), it is abundant on moist floodplains even in the wet CWH and ICH zones. It is most vigorous on sites well supplied with moisture. Jones (1940) noted that the larger coastal var. *laevigatus* is much smaller and resembles the interior var. *albus* when it grows on dry sites. Watson *et al.* (1980) describe it as moderately drought-resistant.

Light Relations: Rowe (1983) describes snowberry as semi-tolerant to shade-tolerant, while Watson *et al.* (1980) indicate that it will grow in partial shade but prefers open sites. Quenet (1973) found that *S. albus* can

[104] Utzig *et al.*, 1983.

survive under crown closures of over 80% in the IDF zone of southeastern B.C., but that very few shrubs were present at this level of canopy closure. Snowberry is rarely found under a coniferous forest canopy in the CWH zone.

GROWTH AND DEVELOPMENT

Snowberry is typically less than 1 m tall at maturity, but can reach 2 m on productive coastal sites (Lyons 1952; Clark 1976). Once established, it spreads outwards to form a low thicket (Lyons 1952; Watson *et al.* 1980). Miller (1977) and Tisdale and Hironaka (1981) report that this spread is achieved by means of rhizomes. MacLean (1969) notes that the roots and rhizomes of snowberry are fibrous and grow mostly between 5 and 13 cm beneath the mineral soil surface. The juvenile twigs are stouter and bear leaves that are larger and more variable in shape than those of older twigs (Jones 1940). A maximum shrub age of 20 years was found on a site in southeastern B.C. (Quenet 1973). Maximum twig biomass was very low compared to other shrub species found on the same site.

Phenology: Bud burst normally occurs in early May in the northern U.S. Rocky Mountains, but can vary by more than a month in either direction depending on elevation and weather conditions. Leaves are full-grown approximately 1 month after emergence. The flowers appear anytime from May to August and may be present as late as September in some locations. Peak flowering time is June and July. Fruit ripening times are equally variable but typically occur during late August and early September, coinciding closely with leaf fall (Schmidt and Lotan 1980). The characteristic white fruit persists on the stems through the winter (Lyons 1952; USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Each berry-like fruit contains two flattened nutlets. A good seed crop is normally produced each year. Seeds are dispersed through the winter by birds and mammals (USDA 1974).

Seed Viability and Germination: Seeds of snowberry remain viable for long periods of time and the species is considered to be a seed banker by Rowe (1983). *Symphoricarpos* seed has a tough outer coat and usually requires warm temperatures followed by chilling to break dormancy (USDA 1974).

Vegetative Reproduction: Snowberry reproduces by means of sprouts from roots and rhizomes as well as by seed (Tisdale and Hironaka 1981; Cholewa and Johnson 1983).

PREDATION AND PESTS

Snowberry is an important browse species for deer and elk, but is not favoured by cattle (Quenet 1973; Watson *et al.* 1980; Tisdale and Hironoka 1981). The fruit is eaten by birds in winter but is apparently not a preferred species (Clark 1976).

EFFECTS ON CROP TREES

Competition: Snowberry is one of the most widespread shrubs in B.C. (Lyons 1952) and is common on a wide variety of forested sites following logging. The nature and magnitude of its competitive effect on conifers has not been documented. In the northern Forest Regions it is not considered to be a major competitor with conifers although it can be locally very abundant (C. Delong and R. Coupé, pers. comm., Nov. 1984; J. Pollack, pers. comm., Jan. 1985). Snowberry is most abundant in the drier forested zones of the southern Interior, and in these areas it may be an important competitor with crop trees, particularly for soil moisture. The canopy of snowberry is generally open, except on some moist sites where it is extremely vigorous, so shading-out of conifers is not as severe as with many associated shrub species. It also does not grow rapidly to great heights, and may quickly be outcompeted by other shrubs and even some trees (J. Pollack, pers. comm., Jan. 1985). Del Moral and Cates (1971) showed that leaf and litter extracts of snowberry can inhibit growth of other plants in laboratory tests, but they could find no evidence of allelopathic interference in the field.

Beneficial Effects: On dry, exposed sites in southern B.C., snowberry may provide shade to seedlings during the early stages of establishment (W.R. Mitchell and D. Lloyd, pers. comm., Nov. 1984). As a rhizomatous species it affords some protection against soil erosion (Watson *et al.* 1980).

RESPONSE TO DISTURBANCE OR MANAGEMENT

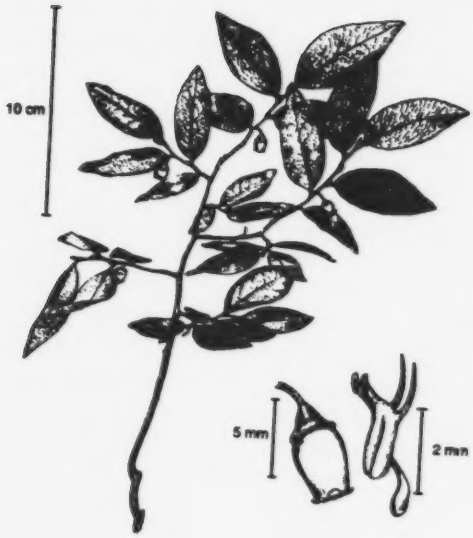
Forest Canopy Removal: Quenet (1973) observed that snowberry cover is inversely related to overstory cover in the IDF zone of southeastern B.C. It is moderately shade-intolerant and can be expected to increase in cover and form low thickets following logging. It does not appear to grow significantly in height in response to canopy removal (J. Pollack, pers. comm., Jan. 1985).

Fire: Snowberry is fairly resistant to severe fires because its roots and rhizomes are located well below the soil surface (MacLean 1969). Following a fire, it will resprout (Tisdale and Hironaka 1981) and spread through rhizomatous growth (Crane *et al.* 1983). Snowberry increased to 15% cover 2 years after burning on a forested site in eastern Oregon (Anderson and Brooks 1975), but Crane *et al.* (1983) reported that initial sprouting in western Montana was slow and the plant only gained rapidly in volume during the third to fifth seasons following a fire. Fire severity and soil moisture content at the time of burning may determine the extent of damage to the rhizome system, and the vigour of sprouting (Miller 1977).

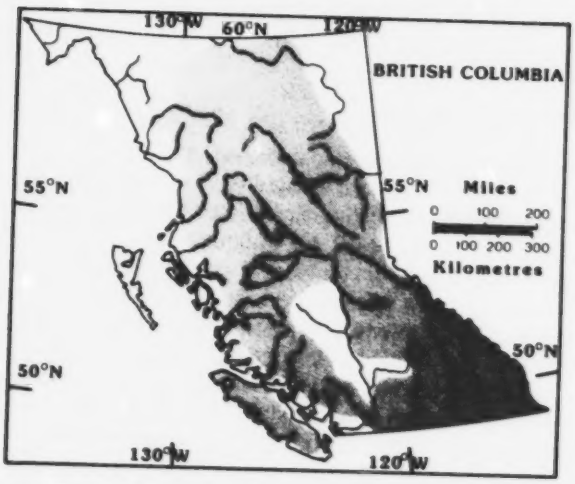
Cutting: Snowberry will resprout after cutting or grazing (Watson *et al.* 1980; Tisdale and Hironaka 1981) and is tolerant of heavy grazing (McLean 1979).

Herbicides: Conard and Emmingham (1983) indicate that snowberry receives very severe injury (90–100%) from spring or fall applications of glyphosate and spring applications of 2,4-D. Late summer or fall applications of 2,4-D cause only moderate injury. In the Vancouver Forest Region, early spring foliar treatments of 2,4-D ester at 3 kg/ha provided excellent control of snowberry (M. Scott, pers. comm., Nov. 1984). In the Prince Rupert Forest Region, snowberry was heavily damaged following a late August foliar spray with 1.5–2 kg a.i./ha of glyphosate (J. Pollack, pers. comm., Feb. 1985).

Soil Disturbance: Snowberry seedlings commonly establish on disturbed soils in the eastern Rocky Mountains (Russell 1979, cited by Watson *et al.* 1980). Soil disturbance can stimulate germination of seed stored in the soil (Rowe 1983). Cover of snowberry was very dense and approximately 1 m tall on a productive, but well-drained floodplain site on the Skeena River within 1 year following heavy soil disturbance. Snowberry had been abundant on the site prior to logging, and most regeneration was probably of sprout origin (authors' personal observation).



Vaccinium membranaceum (black huckleberry).



Distribution of *V. membranaceum* in British Columbia.

Vaccinium membranaceum Dougl.

Black huckleberry
(big huckleberry, thin-leaved huckleberry, mountain blueberry or bilberry)

DESCRIPTION

Black huckleberry is a low to medium-sized, erect, deciduous shrub 0.1–2 m tall. It is densely branched with an extensive network of underground rhizomes. Twigs are somewhat angled in cross-section, the leaves elliptic to oblong with a long, pointed tip and many tiny teeth. Flowers are pinkish bells borne singly on the underside of the twigs. The fruit is a round, purplish black, shiny, edible berry (Szczawinski 1962; Hultén 1974).

Variation: No varieties or subspecies are described in British Columbia (Taylor and MacBryde 1977). This species is very closely related to the *V. globulare* found in southeastern B.C. and east of the Rocky Mountains, and is treated by some authorities as a synonym (Szczawinski 1962).

DISTRIBUTION AND ABUNDANCE

Black huckleberry is found through most of B.C., but is very scattered in the far north, on the north Coast, and in the dry Chilcotin Plateau and Kamloops areas. It is absent from the Queen Charlotte Islands (Calder and Taylor 1968). Black huckleberry is most abundant in mountainous areas of southeastern B.C. in the ICH and ESSF zones, but is abundant in the MH zone and in all cool, moist subzones of the SBS zone.

Altitudinal Range: Black huckleberry grows at moderate to high elevations in B.C. Along the Coast it is found primarily in the subalpine forest above 800 m elevation (Lyons 1952). It is absent from many of the major valleys of the Interior, appearing mainly above 1200 m in the south (Lyons 1952), but moves to lower elevations at northern latitudes and in areas of wetter climate.

HABITAT

Climatic Relations: The distribution of black huckleberry in B.C. appears to coincide with areas receiving at least moderate amounts of snow in winter, and not suffering from significant moisture stress during the summer. Its vigour is significantly reduced in areas of dry climate (R. Coupé, pers. comm., Nov. 1984) and it is absent from southern valleys receiving high summer temperatures and low precipitation. While it is able to tolerate the short growing season found at high elevations in the mountains of southern B.C., it apparently competes poorly in the rigorous climate of the far north. It is replaced by other species of *Vaccinium* in the mild, humid climate found at low elevations on the Coast.

Site and Soil Conditions: Black huckleberry is primarily a species of coniferous forest understories and forest openings on well-drained mountain slopes. Like many other members of its genus in B.C., it is characteristically found on acidic forest soils with a Mor humus. Soils are typically Humo-Ferric Podzols, Dystric Brunisols, and Grey Luvisols on morainal, colluvial, or fluvial parent materials (see e.g., Mitchell and Green 1981; Pojar *et al.* 1984; Delong *et al.*[105]). Minore and Dubrasich (1978) could find no correlation between *V. membranaceum* cover and environmental variables such as slope percent, stoniness, and silt + clay percent of soils in southwestern Washington.

Nutrient Relations: In B.C., *V. membranaceum* is found on a variety of ecosystems described as ranging from poor to rich in nutrients (see e.g., Mitchell and Green 1981; Pojar *et al.* 1984).

Field and greenhouse experiments by Nelson (1974) indicate that additions of ammonium nitrogen improve growth of both roots and shoots of black huckleberry. In the greenhouse studies, nitrogen had a greater effect on growth than either potassium or phosphorus. When nitrogen levels were high, additions of potassium or phosphorus tended to increase growth; when nitrogen levels were low, increasing the levels of potassium and phosphorus either had no effect or reduced growth. For eastern species of *Vaccinium*, ammonium nitrogen (NH_4) is more favourable to growth than nitrate nitrogen ($N0_3$) (Cain 1952). *Vaccinium membranaceum* is tolerant of high levels of manganese but is less tolerant of boron than seedlings of lodgepole pine (Minore 1975). In northern Idaho, Mueggler (1965) found that *Vaccinium* spp. were associated with soils low in potassium.

Nelson (1974) also found that *V. membranaceum* tolerates a broad range of pH. Growth was slightly better at pH 5.0 than at 4.0 or 6.0. At a pH of 3.0, growth was reduced and there was some necrosis of foliage.

[105] Delong *et al.*, 1984.

Foliar concentrations of nitrogen were lowest, and potassium concentrations were highest at pH 3.0. Under field conditions, a high abundance of huckleberry was related to an optimum pH of 5.5 (Minore and Dubrasich 1978).

Water Relations: Black huckleberry is found on sites with a wide range of available moisture (Pojar *et al.* 1982; Angove and Bancroft 1983), but it is most often dominant on mesic and drier ecosystems (see e.g., Brooke *et .al* 1970; Mitchell and Green 1981; Pojar *et al.* 1984; Delong *et al.*[106]).

Light Relations: Black huckleberry commonly grows as an understory plant in coniferous forests but it is most vigorous under partial canopies or in the open. Trees growing under moderately open forest stands seldom produce many berries (Minore 1972), and a dense overstory canopy can eliminate huckleberry production (Minore *et al.* 1979). Light shade may be more favourable than full sunlight (Minore *et al.* 1979). This is probably because shade aids in moisture conservation; however, sunburning of foliage has been reported under high sunlight intensity in other species of *Vaccinium* (Smith 1962).

Temperature Relations: The range of black huckleberry suggests that it must be fairly tolerant of cold temperatures. It is less frost tolerant than *V. deliciosum*, a high altitude species (Minore and Smart 1978). Actively growing seedlings from Oregon suffered no visible damage when subjected to temperatures of 0 and −3°C, but wilted rapidly after exposure to −6 and −9°C. Early and late frosts can significantly damage the plant and destroy buds and flowers. Plants sheltered from cold beneath a protective blanket of snow or under a tree canopy are less susceptible to frost damage (Minore 1972; Nelson 1974; Minore and Smart 1978).

Excellent growth of *V. membranaceum* seedlings occurred in growth chambers set for 14-hour days at 20°C and 10-hour nights at 14°C (Minore *et al.* 1979).

GROWTH AND DEVELOPMENT

Plants of *V. membranaceum* grown from seed first produced blossoms and rhizomes during their third growing season (Minore *et* 1979). Minore (1975) excavated mature plants and found an extensive network of underground rhizomes. There was a complex system of lateral and fine roots, but no taproots. Occasional roots descended to depths of 70–100 cm. The rhizomes were from 1 to 3 cm in diameter and most occurred 8–30 cm below the soil surface. Most of the plant biomass was in the root/rhizome system. Numerous dormant vegetative buds were located along the length of the rhizomes. Shoots arise from these dormant buds, allowing a clone to develop as the rhizomes spread laterally.

The mature height of *V. membranaceum* differs considerably across the province. This species is typically a low shrub, 50 cm or less in height in the SBS and drier ESSF subzones zones of west central B.C. (authors' personal observation) and is reduced to a dwarf shrub in the Chilcotin Plateau (R. Coupé, pers. comm., Nov. 1984). In southern B.C., particularly in areas of moister climate such as the ICH zone, *V. membranaceum* is a taller shrub (Angove and Bancroft 1983), and can reach 2.4 m in height (Clark 1976). Climatic factors, particularly moisture availability, appear to have a major effect on the height growth of this species. Growth of black huckleberry is also subject to extreme seasonal fluctuation (Garrison 1953, cited by Minore 1972).

Phenology: There is little published information regarding the phenology of black huckleberry. It apparently requires a longer period of warm temperatures in spring to stimulate bud burst than the high elevation species *V. deliciosum* (Minore and Smart 1978). Flowering takes place in May and June in B.C. (Lyons 1952) and fruits are ripe in August and September. The date when berries become ripe at a single location varies from year to year depending on weather conditions (Minore and Dubrasich 1978). Cool spring weather delayed ripening of berries in Washington (Minore and Smart 1975).

REPRODUCTION

Seed Production and Dispersal: The round berry of *V. membranaceum* contains numerous small seeds. Fruit production varies considerably from year to year depending on weather conditions, and production can be greatly affected by early fall or late spring frosts. Local environmental factors are less important than weather in determining the size of berry crops (Minore and Dubrasich 1978), but light conditions have a significant effect on berry production. Plants under closed forest produce few, if any berries, and production is heaviest

[106] Delong *et al.*, 1984.

in full sunlight or partial shade (Minore 1972; Minore *et al.* 1979). Berry production can be as much as 720–935 L/ha from berry patches in Oregon and Washington (Minore *et al.* 1979). Dispersal of the seed is primarily by the many mammals and birds that feed on the fruit.

Seed Viability and Germination: The longevity of black huckleberry seed has not been determined, but the seed of most huckleberry species remains viable for many years (Rogers 1974). *Vaccinium membranaceum* seeds require no stratification or scarification and germinate within 16–21 days of sowing (McLean 1967; Minore *et al.* 1979). The seeds must be exposed to at least intermittent light during the entire pregermination period (McLean 1967).

Vegetative Reproduction: The rhizomatous habit of black huckleberry allows it to form spreading clones, and to form new plants when rhizomes become separated from the parent plant through decay or disturbance. Minore *et al.* (1979) report that cuttings taken from rhizomes grow vigorously to produce new plants, but stem cuttings will not root. Miller (1977) indicates that in *V. globulare*, vegetative reproduction through rhizome sprouting is much more important than seedling regeneration following disturbance of an established colony.

PREDATORS AND PESTS

The fruit of black huckleberry is the most heavily harvested *Vaccinium* in western North America. It is prized not only by humans, but also by bears, small mammals, and many bird species. Bears, deer, rabbits, foxes, and many other small mammals browse the twigs and foliage of *Vaccinium* species (Rogers 1974). Use by sheep and cattle is light (McLean 1979; Minore *et al.* 1979).

There are no reports of insect and disease pests.

EFFECTS ON CROP TREES

Competition: Throughout much of the Interior of B.C., black huckleberry is an abundant species on clearcut sites. It is generally not considered to be an important competitor with tree species on its own, but it is a component of the Ericaceous shrub complex that dominates mesic and drier clearcuts in the ESSF zone and some adjacent mid-elevation subzones in the Interior Wet Belt (C. Delong, R. Coupé, and D. Lloyd, pers. comm., Nov. 1984). In these areas it reaches a height of 2 m and can potentially shade out young seedlings, but there is no information describing its impact on seedling growth. In most subzones of the SBS zone in the central and northern Interior, black huckleberry is a small shrub that does not shade out or overtop conifers. Because the species produces a dense network of roots and rhizomes it may compete significantly for moisture and nutrients on dry and nutrient-poor sites.

In Oregon and Washington, where the autecology of *V. membranaceum* has received considerable attention, the species is not perceived as a significant competitor with crop trees. Naturally regenerated conifers quickly overtop the huckleberry bushes, causing a reduction in huckleberry cover and vigour (D. Minore, pers. comm., Dec. 1984)

There is no information regarding possible allelopathic effects of black huckleberry on the growth of conifers and other plant species.

Beneficial Effects: No beneficial effects of *V. membranaceum* on coniferous tree growth are reported in the literature. The dense network of roots and rhizomes may help to reduce soil erosion. The species is highly prized as a berry producer and significant efforts have been made to manage this species as a recreational resource in Oregon and Washington (Minore *et al.* 1979).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Removal of an overstory canopy of trees is reported to favour *V. membranaceum* in the northwestern U.S., increasing growth, cover, frequency, and fruit production (Mueggler 1965; Minore *et al.* 1979; Minore 1984). In B.C., although most observers agree that black huckleberry becomes more vigorous and produces a heavier crop of berries following logging (R. Mitchell and R. Coupé, pers. comm., Nov. 1984), there are no data to indicate that canopy removal causes increases in stem density or seeding-in. *Vaccinium membranaceum* was present but infrequent on four different site types in the SBS zone north of Prince George prior to logging (Eis 1981). Six years after clearcutting, it had not become a significant competitor on any of the site types.

Fire: Research into the effects of fire on western huckleberries has been carried out on *V. membranaceum* in Washington and Oregon (Minore *et al.* 1979; Minore 1984), and on *V. globulare* in Montana (Miller 1977, 1978). The two sets of studies reported different rates of recovery following fire. *Vaccinium globulare* may recover from fire more rapidly than big huckleberry, but differences in burning season and fire intensity probably also account for some of the dissimilarities. The following two paragraphs summarize some of the conclusions that can be drawn from these studies.

In general, *V. membranaceum* recovers rather slowly from fire. Light surface fires, carried out when soils and humus are moist, easily kill above-ground parts of huckleberry, but most rhizomes are buried deep enough to avoid damage. Such fires stimulate prolific sprouting from dormant vegetative buds on the rhizomes. Sprouting occurs almost immediately after an early season burn, or in the season following a late summer burn. Huckleberry cover is lower for the first few years following burning but may return to preburn levels within 3–5 years. Production of flowers and fruit is delayed for several years. Total berry production can be reduced for at least 7 years.

An intense burn, carried out when soils and humus are dry, results in greatly reduced resprouting, and can significantly reduce stem density and cover of huckleberry if heat penetration into the soil is sufficient to kill the rhizomes.

Seedlings of *Vaccinium* spp. are not considered to be important in recolonizing burned sites (Miller 1977).

Cutting and Grazing: Black huckleberry shrubs did not respond vigorously to pruning treatments that removed 50–80% of top growth (Minore *et al.* 1979). In contrast, clipping significantly increased the number of new shoots in *V. globulare* (Miller 1978). The time of clipping did not significantly affect the number of shoots produced. Miller predicted that sprouting following hand cutting of *V. globulare* would be much less than the sprouting following a light fire.

Heavy grazing of huckleberry fields by sheep did not damage black huckleberry plants. The effects of sheep browsing were more than offset by the nitrogen added as sheep manure (Minore *et al.* 1979). In an earlier study,[107] grazing by sheep reportedly produced thriftier, more vigorous huckleberry growth by lightly browsing the shrubs and reducing competition from other vegetation.

Herbicides: In Oregon, a midsummer application of 2,4-D ester at 6.38 kg/ha significantly reduced huckleberry cover (Minore *et al.* 1979). However, herbicide-damaged plants recovered faster than plants damaged by burning in the same area. Black huckleberry was very tolerant of glyphosate applied aerially at 2.25 kg/ha near Prince George (Expert Committee on Weeds 1984). Newton (pers. comm., Dec. 1984) describes black huckleberry as very resistant to glyphosate and only moderate susceptible to midsummer applications of triclopyr.

Soil Disturbance: Discing apparently stimulated rhizome sprouting of V. membranaceum in Washington (Minore *et al.* 1979).

Fertilization: Fertilization with ammonium sulphate significantly increases vegetative growth of black huckleberry (Nelson 1974).

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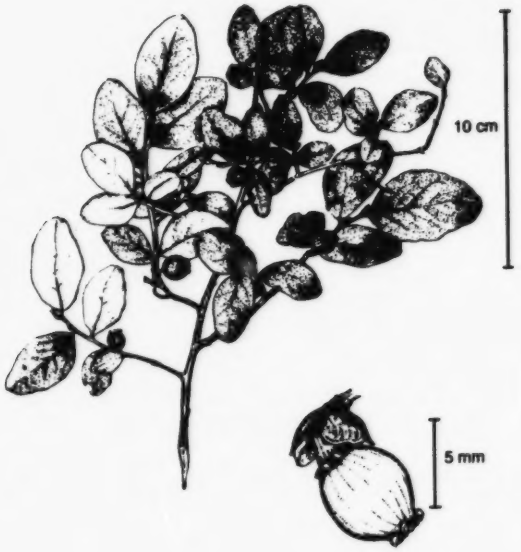
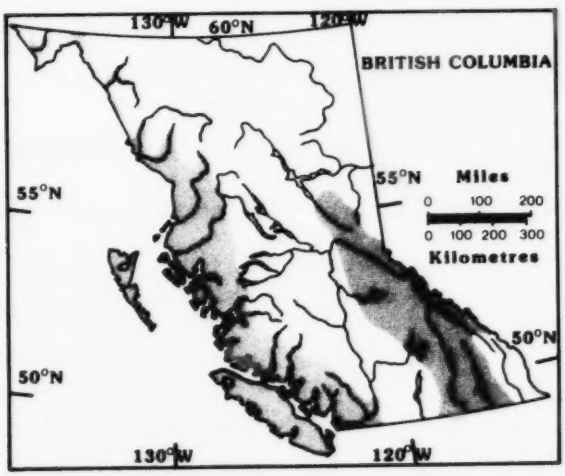
[107] K.C. Langford. 1942. Effect of grazing on huckleberry production. U.S. Dep. Agric., For. Serv. Unpublished report, cited by Minore 1972. On file at Mount Adams Ranger District, Trout Lake, Wash.



Vaccinium ovalifolium (oval-leaved blueberry).



Distribution of *V. ovalifolium* in British Columbia.

Vaccinium ovalifolium Sm. — Oval-leaved blueberry

DESCRIPTION

Oval-leaved blueberry is a spreading, diffusely branched, deciduous shrub, 1–2 m tall. Twigs are slender, reddish brown and grooved. The leaves are thin, oval and rounded at the base and tip. The pink urn-shaped flowers appear before the leaves on the underside of the twigs. The berry is round and blue to bluish black, with a distinct frosty bloom (Szczawinski 1962; Viereck and Little 1972).

Variation: No varieties or subspecies of oval-leaved blueberry are described in British Columbia (Taylor and MacBryde 1977). It may hybridize with *V. alaskaense* on the Coast where these two species occur together (Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Oval-leaved blueberry is found along the entire length of the B.C. coast, and penetrates inland for some distance on the east side of the Coast Mountains. It is also found in moist mountainous areas of the Interior Wet Belt, as far north as Williston Lake, but is absent from the central and dry southern Interior and from the far north (Szczawinski 1962). Oval-leaved blueberry is most abundant in the CWH, MH, and CCPH biogeoclimatic zones on the Coast and in the ICH and moist southeastern subzones of the ESSF in the Interior. It is also present in some wetter subzones of the SBS.

Altitudinal Range: Oval-leaved blueberry is present from sea level to timberline along the Coast, except in the Georgia Strait area where it becomes important at middle elevations. Throughout most of its range in the southern and central Interior, it is present from mid-elevations to timberline, but is absent from major valley bottoms.

HABITAT

Climatic Relations: Oval-leaved blueberry apparently favours a humid to perhumid climate in which it is unlikely to suffer from moisture or high temperature stress during the summer. It is found in all areas of the province receiving either abundant rain or snow, except the far north, where the climate presumably is too severe.

Site and Soil Conditions: Species of the genus *Vaccinium* are described as being "exacting in their site requirements" (USDA 1974). In B.C., oval-leaved blueberry is typically associated with hemlock-dominated coniferous forests that have a thick acidic mor humus and a podzolic soil. It is found on a wide variety of parent materials and is frequently rooted in organic or decaying wood substrates (see e.g., Brooke *et al.* 1970; Annas and Coupé (editors) 1979; Klinka *et al.* 1979; Haeussler *et al.* 1984).

Nutrient Relations: Oval-leaved blueberry is found on sites ranging from very poor (oligotrophic) to very rich (eutrophic) in nutrients (see e.g., Klinka 1977*b*; Utzig *et al.*[108]). The pH of the rooting zone in ecosystems where it is abundant is usually low (i.e., pH <5) (see e.g., Haeussler *et al.* 1984; Meidinger *et al.* 1984; Coupé and Yee (editors)[109]).

Water Relations: Oval-leaved blueberry is abundant on sites with a wide range of available moisture, from very rapidly drained (xeric) to poorly drained (hygric) (Klinka 1977*b*; Angove and Bancroft 1983); however, it is most abundant and dominant on mesic and drier sites where the shrub layers are relatively species poor. On poorly drained sites it is usually found on elevated microsites (Haeussler *et al.* 1984).

Light Relations: Oval-leaved blueberry is a very shade-tolerant species. It will survive under the low light intensities found under a hemlock forest canopy, but growth rates and plant vigour under heavy shade are poor (P. Alaback, pers. comm., Dec. 1984). Cover and vigour of the species are greatest under an open tree canopy or on cutover forest land where it may form a nearly continuous shrub layer (Viereck and Little 1972). Camp (1942) describes it as less shade-tolerant than *V. alaskaense*, a common associate in coastal forest.

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

Oval-leaved blueberry is a rhizomatous species with an open, spreading crown that can reach heights of over 2 m under favourable conditions. The maximum annual growth rate of shoots in Alaska is approximately 30

[108] Utzig *et al.*, 1983.
[109] Coupé and Yee (editors), 1982.

cm. The growth rate of seedlings established under a dense forest canopy is almost insignificant; seedlings can still be in the cotyledon stage after two growing seasons. Under low light conditions, the seedling can take on a juvenile form which has evergreen leaves and a semi-prostrate growth form. This juvenile form does not appear under favourable growing conditions in a greenhouse, and when the overstory shade is removed through windfall or logging, the plant soon takes on the erect, deciduous "adult" growth habit (P. Alaback, pers. comm., Dec. 1984)

Phenology: In coastal Alaska, flowering occurs during April and May before the leaves emerge (Viereck and Little 1972). Bud burst occurs in May and is followed by a period of rapid growth. Most vegetative elongation is complete by mid-June, but stems continue to increase in diameter until mid-July (P. Alaback, pers. comm., Dec. 1984). Leaf sensecence did not begin until early September on the central B.C. coast, and some leaves were still on the shrubs at the end of October (T. Hamilton, unpublished data, 1984, B.C. Min. Environ. Victoria, B.C.). Ripe berries are present beginning in late June on the central B.C. coast (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.), and from mid-July to August in Alaska (Viereck and Little 1972).

REPRODUCTION

Seed Production and Dispersal: Light is critical for fruit production. Oval-leaved blueberry will only produce fruit in fairly open areas. In Alaska, heavy fruiting occurs only in large forest openings or along forest margins. A single fruit can contain 150 seeds and the total seed production in years of good berry crops is enormous (P. Alaback, pers. comm., Dec. 1984). Seeds are dispersed by birds and mammals that feed on the fruit.

Seed Viability and Germination: Seeds of oval-leaved blueberry are described as remaining viable for up to 12 years in storage (USDA 1974); however, Alaback (pers. comm., Feb. 1985) believes that in Alaska at least, their viability is short-lived. The seeds have a short dormancy period and will germinate well after 15 days of warm temperatures followed by just 15 days of chilling (USDA 1974).

Germination rates of approximately 50–60% are obtained under favourable conditions. A minimum of 2% of full light is needed for germination to occur, so seedlings are able to germinate under a forest canopy. The seed will germinate on a wide variety of substrates including mineral soil, moss, bare humus, and decaying wood, but conditions for subsequent seedling establishment are more critical. Survival is best in open old-growth stands and in clearcut areas, and poor in dense immature forests. Survival is best on humus with no moss cover and poorest on mineral soil (P. Alaback, unpublished data, 1984, Oregon State Univ., Corvallis, Oreg.).

Alaback speculates that the regeneration strategy of oval-leaved blueberry in southeastern Alaska is like that of western hemlock. It is a "seedling banker" (v. Grime 1979), which produces shade-tolerant seedlings that persist for long periods of time in the understory until a disturbance creates favourable conditions for growth and seed production. Very few seedlings germinate under the undisturbed forest canopy, but the species often germinates in small windthrow openings. Stored, ungerminated seed is not considered to be important for regeneration of the species.

Vegetative Reproduction: Oval-leaved blueberry regenerates vegetatively by means of rhizomes (and layering?). Vegetative reproduction is the primary means by which this species survives for long periods of time in the absence of disturbance. Expansion of existing colonies also takes place by means of rhizomatous shoots (P. Alaback, pers. comm., Dec. 1984).

PREDATORS AND PESTS

Oval-leaved blueberry is browsed in winter by deer, mountain goat, and elk (Viereck and Little 1972). The foliage and fruit are eaten by bears. *Vaccinium* berries are a favoured food of many birds and small mammals (Rogers 1974).

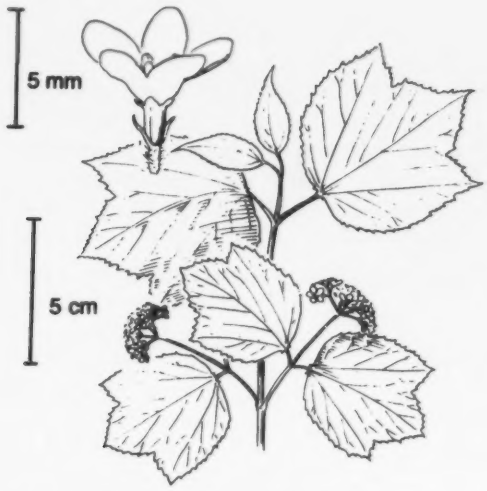
EFFECTS ON CROP TREES

Although oval-leaved blueberry is an abundant and often dominant shrub in both coastal and wet Interior forests, it is not thought of as an important competitor with coniferous trees. There are no data to indicate what negative or beneficial effects this species has on the growth of crop trees.

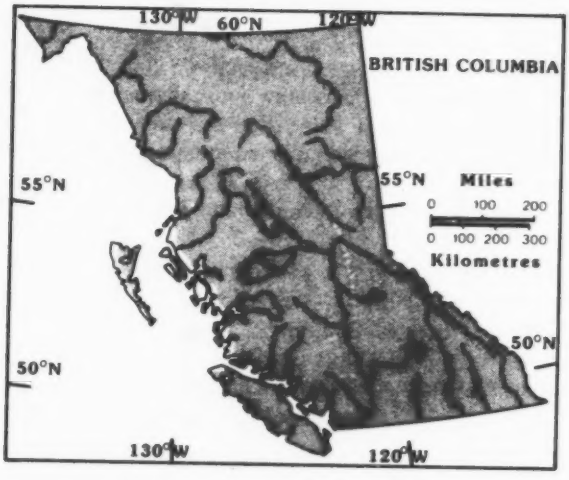
RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: In the SBS zone north of Prince George, *V. ovalifolium* did not increase dramatically on any of four site types following logging, but it was a common shrub on the Devil's Club site type (Eis 1981). In a thinning study in southeast Alaska, *V. ovalifolium* seedlings were scattered on a site where trees had been spaced to 2.4 × 2.4 m. They were more abundant at the wider spacings and produced flowers at the 4.9 × 4.9 m spacing (P. Alaback, 1984, unpublished data, Oregon State Univ., Corvallis, Oreg.).

Fire: On a study site in southwestern B.C., oval-leaved blueberry was a common element of the post-logging preburn plant community (Lafferty 1972). In the first growing season after a burn of moderate intensity, blueberry was absent, and three growing seasons after burning, it had not regained its vigour.



Viburnum edule (highbush-cranberry).



Distribution of *V. edule* in British Columbia.

Viburnum edule (Michx.) Raf.

Highbush-cranberry
(squashberry)

DESCRIPTION

Highbush-cranberry is a straggling to erect, multistemmed deciduous shrub, 0.5–3 m tall. Stems have opposite branching and shiny red buds. The leaves are irregularly shaped with three shallow, toothed lobes, and become bright red in fall. The small, dense, flat to rounded inflorescence has white flowers. The fruit, red drupes with a large flattened stone, remain on the twigs over winter (Hultén 1974; UBC Bot. Garden 1977).

Variation: No subspecies or varieties are described from British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Viburnum edule is found throughout B.C. to the Yukon border, but is absent from the dry southern Interior and higher subalpine and alpine zones (Lyons 1952). It is found in all biogeoclimatic zones except the PPBG and AT, but is uncommon to rare in the CCPH, MH, SWB, and higher ESSF zones. It is particularly abundant in the central and northern Interior of the province in the SBS and BWBS zones.

Altitudinal Range: Highbush-cranberry ranges from sea level to approximately 1500 m in B.C. (UBC Bot. Garden 1977).

HABITAT

Climatic Relations: Highbush-cranberry is found throughout northern North America but is primarily a species of the boreal climatic region. The southern extent of its range appears to be limited by high temperatures and low humidity. It appears to tolerate most of the climates present in B.C. except the very hot, dry climate of the southern Interior valleys and the severe alpine climate. It is uncommon in extremely wet coastal areas.

Site and Soil Conditions: Most *Viburnum* species prefer moist, well-drained soils, but soil texture is less critical than for many other genera (USDA 1974). In B.C., *V. edule* is a species of moist, forested slopes, stream or lake margins, and gravelly or rocky banks (Clark 1976; UBC Bot. Garden 1977). It is found on a wide range of parent materials and soil types including Luvisols, Brunisols, Humo-Ferric Podzols, Regosols, and Gleysols. Its best development occurs on floodplain sites where it can be a dominant shrub under a black cottonwood or balsam poplar overstory (see e.g., Zasada *et al.* 1981; Pojar *et al.* 1984; Trowbridge *et al.*;[110] C. Delong, unpublished data, 1983, B.C. Min. For., Prince George, B.C.).

Nutrient Relations: Highbush-cranberry grows best in rich soil with a pH of about 6.5 (UBC Bot. Garden 1977), but in nature it is usually found on soils with greater acidity (see e.g., Pojar *et al.* 1984; C. Delong, unpublished data, 1983, B.C. Min. For., Prince George, B.C.). It is typically found on sites characterized as medium (mesotrophic) to very rich (eutrophic) in nutrients (Comeau *et al.* 1982; Pojar *et al.* 1982).

Water Relations: Throughout B.C., highbush-cranberry is associated with moist soils (Lyons 1952; UBC Bot. Garden 1977). It grows on sites with a submesic to subhydric moisture status in areas of moist climate and at northern latitudes, but is restricted to subhygric and wetter moisture regimes in drier climates in central and southern B.C. (Comeau *et al.* 1982; Pojar *et al.* 1982; Angove and Bancroft 1983).

Light Relations: Highbush-cranberry is described as semi-tolerant to shade-tolerant by Rowe (1983), and several authors report that it prefers shady locales (Lyons 1952; Clark 1976; UBC Bot. Garden 1977). It is more commonly found growing in the open at high elevations (Lyons 1952), and probably also at northerly latitudes. Highbush-cranberry is a common understory species in deciduous and coniferous forests (see e.g., Pojar *et al.* 1984; C. Delong, unpublished data, 1983, B.C. Min. For., Prince George, B.C.), but like many shrub species it probably attains its best development under full sunlight provided that it is not exposed to excessive evapotranspirative stresses.

Temperature Relations: The presence of highbush-cranberry at northern latitudes indicates that it must have high frost tolerance and an ability to grow at low soil and air temperatures. Its preference for shady locations in the southern half of its range may indicate that it is not tolerant of high temperatures.

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[110] R. Trowbridge, J. Pojar, and T. Lewis. 1983. Interim classification of the Boreal White and Black Spruce biogeoclimatic zone in the Prince Rupert Forest Region. B.C. Min. For., Smithers, B.C. Unpublished report.

GROWTH AND DEVELOPMENT

There is little published information regarding the growth and development of highbush-cranberry. It is a multistemmed shrub with a rather scraggly habit because of frequent natural layering. Underground rhizomes are present to a depth of 20–30 cm beneath the soil surface.[111] It can be as small as 0.15 m at maturity or as tall as 3.5 m (UBC Bot. Garden 1977), but average heights are in the range of 0.75–2 m (Clark 1976). Highbush-cranberry grows at a moderate rate throughout its life (UBC Bot. Garden 1977). It can reach a height of 1 m in 4 years in Alaska (Zasada *et al.* 1981).

Phenology: Observations in the Kimsquit valley on the central B.C. coast indicate that leaf flush occurs in April or early May, but leaves are not fully expanded until late May. Leaf senescence and abscission appear to take place earlier on highbush-cranberry than on most associated shrubs. (T. Hamilton, unpublished data, 1984, B.C. Min. Environ., Victoria, B.C.). In general, flowering occurs from May to July. Fruits are ripe from late August to October, but remain on the twigs throughout the winter (UBC Bot. Garden 1977).

REPRODUCTION

Seed Production and Dispersal: Fruits of highbush-cranberry are first produced when the plant is approximately 5 years of age, but are then produced in quantity nearly every year. Each fruit contains exactly one seed (UBC Bot. Garden 1977). Dispersal is by birds and mammals that feed on the fruit through the winter, and by gravity (USDA 1974).

Seed Viability and Germination: Seeds of highbush-cranberry remain viable in storage for up to 10 years (UBC Bot. Garden 1977). Rowe (1983) considers highbush-cranberry a seed-banking species. The seeds of *Viburnum* spp. are difficult to germinate because they have both seed coat and embryo dormancy, but treatment of the seed coat has not been shown to improve germination. Best germination normally occurs if a period of warm temperatures is followed by several months of near freezing temperatures. Germination is slow even after this treatment, and in nature most northern species of *Viburnum* do not germinate until the 2nd year after fruit ripening (Giersbach 1937; USDA 1974; UBC Bot. Gardens 1977).

Vegetative Reproduction: Highbush-cranberry regenerates vegetatively by natural layering, and by sprouting from damaged root stocks and stem bases (UBC Bot. Garden 1977; Foote 1983). The plant is rhizomatous (Holloway and Zasada 1979; Parminter[112]), but there is no evidence that it spreads laterally from the parent plant by means of root or rhizome suckers. Foote (1983) states that new shoots of *V. edule* that emerged following fire were found near the base of a burned plant. Dormant cuttings taken in fall root poorly, but actively growing cuttings produce prolific roots; rhizome cuttings can be readily propagated (Holloway and Zasada 1979).

PREDATORS AND PESTS

Highbush-cranberry is browsed by deer, moose, rabbits, and beavers, and its fruits are eaten by deer, small mammals, and birds (UBC Bot. Garden 1977).

A leaf spot (*Ascochyta viburni*) has been found on *V. edule* on the Coast, while a rust (*Puccinia linkii*) is present in northern B.C. (Toms 1964). Neither of these diseases is considered serious. Aphids, thrips, spider mites, and scale are are likely to occur on *Viburnum* (UBC Bot. Garden 1977).

EFFECTS ON CROP TREES

Competition: Highbush-cranberry is not considered to be a primary competitor with coniferous trees in B.C. However, throughout much of its range it is a common member of the complex of brush species that appears on very moist, productive sites, particularly on floodplains or under a deciduous canopy. It is most abundant and dominant in northern subzones of the SBS and in the BWBS zone throughout northern B.C., where it can compete significantly with natural or planted white spruce.

Beneficial Effects: No information.

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[111] J. Parminter. 1983. Fire ecological relationships for the biogeoclimatic zones and subzones of the Fort Nelson Timber Supply Area. Summary Report. B.C. Min. For. Protection Branch, Victoria, B.C. Unpublished report.

[112] Ibid, 1983.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: There are varying reports in the literature of the response of highbush-cranberry to canopy removal. In the SBS zone north of Prince George, Eis (1981) found that although highbush-cranberry was present on all four site types prior to logging, it had not become a significant component of the vegetation on any of these site types 6 years after clearcutting. In the sub-boreal forest of Alberta, *V. edule* had a substantially lower cover in 6- to 12-year-old clearcut areas than in the mature lodgepole pine forest (Corns and LaRoi 1976). In contrast, density of this species increased dramatically following logging of a balsam poplar stand in Alaska (Zasada *et al.* 1981). Highbush-cranberry was one the the dominant shrubs on the logged sites and reached 1 m in height within 4 years.

Fire: In the boreal forest of interior Alaska, *V. edule* resprouts within weeks of a fire on white spruce sites and is one of the dominant post-fire shrubs (Rowe 1983). The underground rhizomes will survive shallow burns and sprouting occurs at the base of the fire-killed above-ground stem.[113] Regeneration of highbush-cranberry seed stored in the soil is favoured by fires of low severity and short duration that remove very little of the humus layer (Rowe 1983).

Herbicides: The effects of herbicides on highbush-cranberry have received very little attention. In a study conducted near Dawson Creek, B.C., a young aspen – balsam poplar stand was aerially sprayed in June with 3 kg/ha glyphosate (Expert Committee on Weeds 1984). Highbush-cranberry was 95% defoliated and suffered heavy mortality. Hexazinone does not appear to give significant control of this species (Expert Committee on Weeds 1984).

Soil Disturbance: Highbush-cranberry increased less on a winter logged balsam poplar stand than on one that had been summer logged (Zasada *et al.* 1981). Soil disturbance was probably higher on the summer logged site and may have stimulated resprouting of the shrub. Scarification does not appear to have enhanced the cover of highbush-cranberry on clearcut areas near Edson, Alberta (Corns and LaRoi 1976).

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[113] Parminter, 1983.

4 RESEARCH NEEDS

Preparation of this literature review and its companion report, "A Preliminary Guide to the Response of Major Species of Competing Vegetation to Silvicultural Treatments" (Coates and Haeussler 1985), has revealed several major gaps in the knowledge of both the autecology of the selected species, and of their response to silvicultural treatments in British Columbia. Ten topics relating to the species in this publication are identified as meriting further research. (Some of these have been previously addressed by Conard (1984) in a problem analysis of forest vegetation management in British Columbia.)

1. Further autecological studies of all species are warranted. There are information gaps in our knowledge of each species in the literature review. However, there are several poorly documented species for which basic information about growth and development, reproductive strategies, and habitat interactions is required. These are:

   Rubus parviflorus
   Lonicera involucrata
   Rhododendron albiflorum
   Ribes bracteosum
   Athyrium filix-femina
   Alnus viridis and *A. incana* ssp. tenuifolia
   Menziesia ferruginea
   Vaccinium spp.
   Viburnum edule

   Rubus parviflorus should receive first priority for basic autecological investigations because of its widespread importance as a competitor.

2. Studies that document the nature of interactions between the non-crop species and coniferous crop trees are needed. For many species, the mechanism and magnitude of competition with crop trees are unknown.

3. Studies to determine the rate of height growth and the rate of percent cover increase for individual species following disturbance on specific problem ecosystems are required.

4. Combination or multiple treatments can potentially control many species of competing vegetation. Combinations of cutting, chemical treatment, prescribed burning, and mechanical site preparation should be tested and compared to the effectiveness of single treatments.

5. A report that summarizes the results of herbicide trials and experiments on a species-by-species basis using a standardized format should be prepared. This report could have a format similar to the computer listing of Miller and Kidd (1983), and should allow for frequent updating.

6. Herbicide efficacy studies are needed for individual species cn a variety of habitats, and for a range of life cycle and phenological stages.

7. Studies are needed to determine the effectiveness of manual cutting treatments. Further research is needed into the effect of age, season, stump height (possibly angle), and multiple cuttings on mortality rates and sprout or sucker vigour of individual species. Potential candidates for manual control include: *Rhododendron albiflorum, Menziesia ferruginea, Vaccinium* spp., *Alnus viridis, A. incana* ssp. *tenuifolia, Lonicera involucrata,* and possibly *Cornus sericea, Symphoricarpos albus,* and *Viburnum edule.*

8. Studies should be carried out to determine whether *Alnus viridis* or *A. incana* are beneficial to the growth of crop trees on nitrogen-deficient Interior sites.

9. Pre-harvest treatments (i.e. girdling, chemical applications, or cutting) of deciduous trees growing in mixture with conifers may be effective. Studies are needed to document the effect of such treatments on the subsequent sprouting, suckering, or seeding-in of deciduous species.

10. Where possible, efforts should be made to co-ordinate any research on a particular species, so that regional differences in the species' autecology and response to silvicultural treatments can be documented.

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